Biogeographical and Evolutionary Relationships Among Central American Small-Eared Shrews of the Genus Cryptotis (Mammalia: Insectivora: Soricidae)

by Neal Woodman

B. A., Earlham College, 1976

M. S., The University of Iowa, 1982

M. Phil., University of Kansas, 1986

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Professor in Charge

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ABSTRACT.--Small-eared shrews of the genus *Cryptotis* have a distribution that extends from southernmost Ontario and across much of the eastern half of the United States south to the northern Andean highlands. The genus attains its greatest diversity in Mexico and Central America, where eight species generally have been recognized. My studies of geographical and elevational distribution and correlated morphological variation indicate that *Cryptotis* is much more diverse and speciose than previously considered. I recognize 19 species in this same region, and I suggest that there is potential for even greater species-level diversity. This is mostly a result of prehistoric isolation of populations in restricted highland areas, subsequent morphological divergence, and speciation. This brings the total number of species of *Cryptotis* to 25; there is a total of 36 monotypic species and subspecies.

Phylogenetic analysis of the genus *Cryptotis* using a matrix of 19 transformation series indicates three well-supported lineages occur within the genus: the *C. parva* group, consisting of *C. parva* and all of its subspecies; the *C. nigrescens* group, which includes *C. magna* in

addition to species once considered subspecies of C. nigrescens; and the C. thomasi group, which now includes C. gracilis, C. endersi, and members of the C. mexicana group, as well as most South American species. Relationships among the three lineages are uncertain, but the C nigrescens most likely shares a sistergroup relationship with either the C. parva group or the C. thomasi group. Within the C. nigrescens group C. magna has a sister group relationship with C. mayensis and C. merriami.

Biogeography of the genus Cryptotis is complex, and it appears that ancestral patterns of divergence have been obscured by subsequent expansion and contraction of species ranges.

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INTRODUCTION

Small-eared shrews of the genus Cryptotis are poorly known despite a wide distribution extending from southern Ontario, across much of the eastern and midwestern United States, through portions of Mexico and Central America, to the northern Andean highlands (Fig. 1). The most familiar species, particularly to North American biologists, is Cryptotis parva, whose range includes the eastern half of the United States. Most of our current information about Cryptotis comes from studies of this one species (e.g., Whitaker, 1974), yet the genus attains its greatest diversity in Mexico and Central America, where it remains mostly unstudied. In their synopsis of North American mammals, Hall and Kelson (1959) recognized 25 species of Cryptotis in Mexico and Central America. Choate (1970), in his landmark revision of the Middle American members of the genus, recognized eight species in this same region, and his taxonomy has been followed by subsequent authors, including Hall (1981), Honacki et al. (1982), Corbet and Hill (1991), and Nowak (1991).

Recent collecting has made available for study important new specimens of Cryptotis, particularly from central and southern Mexico, Honduras, Costa Rica, and

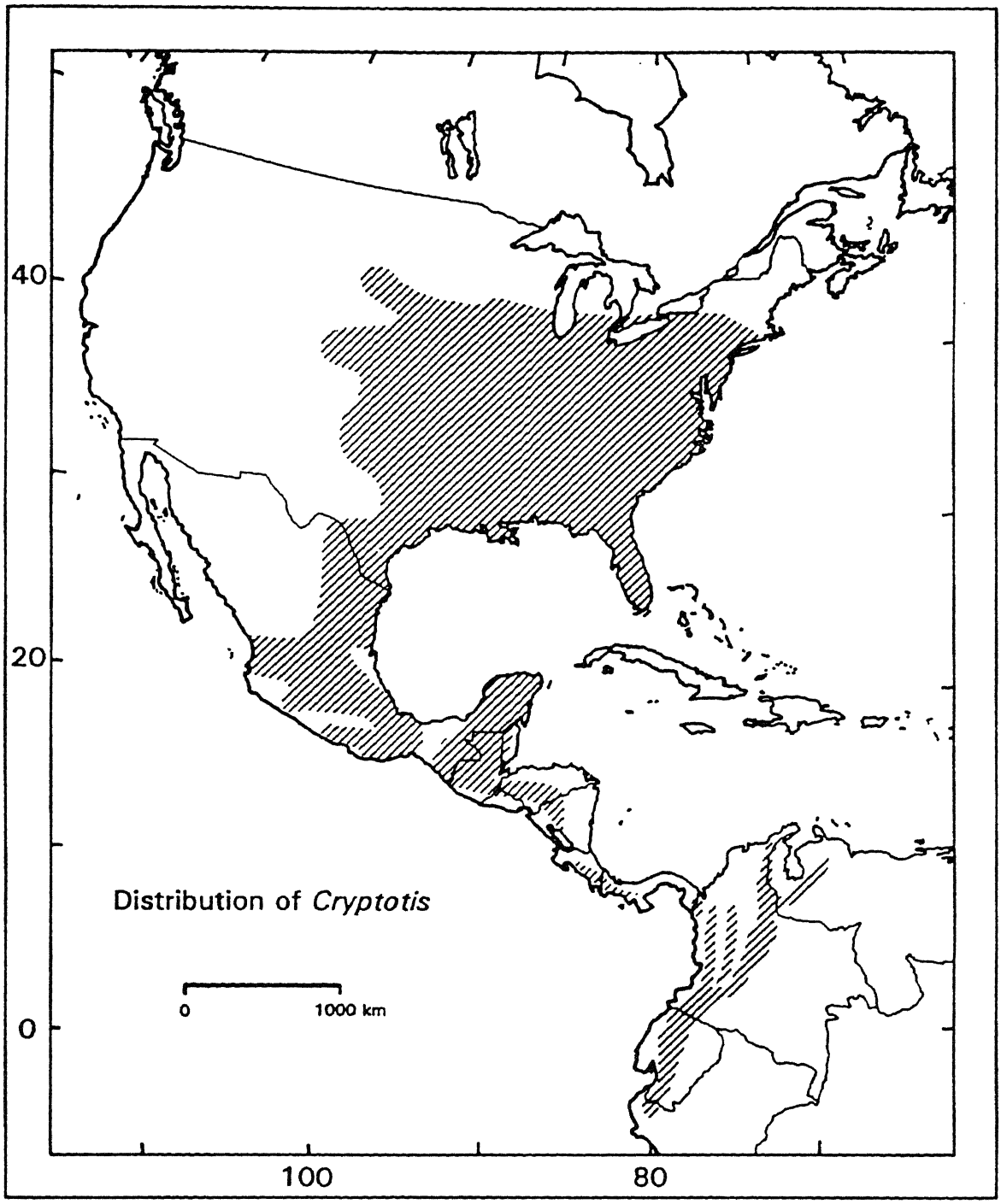

Figure 1. Distribution of small-eared shrews, genus Cryptotis.

Panama. Many specimens are from previously uncollected areas. These new specimens now permit a closer review of geographic variation within members of the genus, and a more complete evaluation of the taxa contained therein. This end is furthered by new concepts of species and means of establishing testable hypotheses of species phylogenetic interrelationships, which were not in general use 20 years ago. As a result, Cryptotis is proving to be much more diverse and speciose than previously considered. This is a result of prehistoric isolation of populations in restricted highland areas, subsequent morphological divergence (and inferred genetic divergence), and speciation.

The study of the patterns of divergence and distribution through biogeography and phylogenetic analysis are important to understanding the historical development of Cryptotis. These results also will prove useful in understanding the evolution of the Latin American biotic communities in which these shrews occur.

The following chapters have been prepared to stand alone as individual manuscripts. Thus, some repetition, particularly in the introductory statements, will be apparent. Although each addresses a unique topic, together they serve to redefine our understanding of Mexican and Central American species of small-eared

shrews.

The first chapter describes a new species of Cryptotis from Honduras, based on a specimen which long was misidentified as a C. gracilis. This misidentification was confusing biogeographically, and the study of this specimen and two paratypes clarifies some important questions about the distributional patterns seen in the genus. The next three chapters review the taxonomic status of the C. gracilis complex, the C. goldmani/goodwini complex of large-footed shrews, and the C. nigrescens complex, respectively. The purposes of these chapters are to: 1) redefine the recognized diversity within each of the species complexes; 2) redescribe and illustrate the previously described species in each complex; 3) provide descriptions and illustrations of several species new to science; 4) provide a key to species within each complex; and 5) review the available information on reproduction, elevational distribution, and habitat for the members of each complex. The following chapter reevaluates fossil remains of Cryptotis from a cave on the Yucatan Peninsula of Mexico and their relationship with modern species. The final chapter is a preliminary phylogenetic analysis of members of the genus Cryptotis based on morphological characteristics, and in it I

propose an hypothesis of evolutionary relationships among these taxa. Following this is a discussion of the results of the preceding chapters and a conclusion. An appendix is included at the end, which summarizes the taxonomic history of the genus Cryptotis, evaluates the correct gender of the name Cryptotis based on its Greek roots, and provides a listing of all type specimens and all proposed names within the genus.

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A NEW SPECIES OF SMALL-EARED SHREW, GENUS *CRYPTOTIS* (INSECTIVORA: SORICIDAE), FROM HONDURAS

Small-eared or least shrews of the genus *Cryptotis* (Insectivora: Soricidae) are widely distributed in North America, Central America, and northern South America. They are found in extreme southern Ontario, across much of the eastern and midwestern United States, through eastern, central, and southern Mexico, at high elevations in Central America, and in the northern Andean highlands. The systematics of the Neotropical species are problematic, in part because few specimens have been available, and individual and geographic variation has been difficult to evaluate. Choate (1970) recognized eight species of *Cryptotis* from Mexico and Central America. His monograph was the first comprehensive revision of any group in the genus, providing an important framework for study of these shrews.

One of the most poorly known species of Neotropical *Cryptotis*, *C. gracilis*, was reported by Choate (1970) as ranging from southern Honduras to western Panama. Among the specimens he referred to *C. gracilis* were one specimen from southern Honduras, 38 from Costa Rica, and three from western Panama. The acquisition of

additional specimens of C. gracilis from Costa Rica and Panama prompted me to reexamine this species throughout its range. Detailed comparison of the single specimen from Honduras with Costa Rican and Panamanian C. gracilis reveals that it represents a previously unrecognized species. Acquisition of two additional specimens of the new species during the course of my study confirms its distinctiveness. The purposes of this paper are to describe and illustrate this new small-eared shrew and to briefly document its relationship to other members of the genus Cryptotis.

Methods

All external and craniodental measurements reported herein are in millimeters (mm). External measurements of the holotype were taken on the fluid preserved specimen with the skull removed. External measurements of the two paratypes were taken on the fluid preserved specimens with the skulls in place; subsequently, I removed the skulls and all craniodental measurements were taken from cleaned skulls. Sixteen cranial measurements were taken to the nearest 0.1 mm using either a hand-held dial caliper or an ocular micrometer in a Wilde M50 binocular microscope. Cranial measurements follow Choate (1970), in part, and

mandibular measurements follow Jammot (1973), in part. All craniodental measurements are further diagrammed in a forthcoming manuscript (Woodman and Timm, submitted) on geographical variation in C. gracilis. Dental terminology follows Choate (1970). Capitalized color names are from Ridgeway (1912).

Multivariate analyses were carried out using the University of Kansas Academic Computing Services' IBM 3031AP processor running a VM/CMS operating system. Discriminant function analysis (BMDP7M) was performed on 8 cranial and 7 mandibular measurements (Table 1; condylobasal length was not used because it was not measureable on all specimens) to discriminate among C. gracilis (n = 20), C. nigrescens merriami (n = 13), and C. parva orophila (n = 16). The holotype and one paratype of the new species were inserted into the discriminant function model as unknowns to evaluate their similarities to other species from the region. As a further, more conservative test, principal components analysis (BMDP4M) was run using the same 15 variables as for discriminant fucntion analysis. The holotype and one paratype of the new species and all specimens of C. gracilis, C. nigrescens merriami, and C. parva orophila were included in this analysis as a single population.

Specimens from the following institutions (followed

by their acronyms) were examined in this study: American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); University of Kansas Museum of Natural History, Lawrence (KU); Louisiana State University, Baton Rouge (LSU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Universidad Nacional Autónoma de Honduras, Tegucigalpa (UNAH); National Museum of Natural History, Washington, D.C. (USNM).

Cryptotis hondurensis, Woodman and Timm, 1992

Figs. 2, 5B, 6B

Cryptotis gracilis.--J. R. Choate, 30 December 1970, Univ. Kansas Publ. Mus. Nat. Hist. 19:282-285.--E. R. Hall, 3 April 1981, The Mammals of North America, 2nd ed., 1:63-64.

Holotype.--Skull of adult female with body preserved whole in alcohol, KU 106941; collected 5 July 1966 by William E. Duellman (collector number M-1405). Skull complete and unbroken; body intact, but with a patch of hair missing from venter.

The collection date is given in the original field catalog as 6 July 1966. However, the collector pointed

out to me that this is probably the date he entered the specimen into his catalog. His original field notes indicate that the specimen was collected 5 July.

Paratypes.--(2): skull of adult female with body preserved whole in alcohol, FMNH 86886; collected in the 1950s by Luis and Terua Williams. Skull lacking braincase; body intact.

Skull of juvenile male with body preserved whole in alcohol, UNAH (no number); collected 7 February 1988 by E. Frainvilledo (lot number 977). Skull lacking braincase and portions of palate and rostrum; body intact, but with a patch of hair missing from venter.

Type locality.--Honduras: Francisco Morazán Department; 12 km WNW of El Zamorano, W slope of Cerro Uyuca [= Cerro Oyuca; ca. 14°05'N, 87°06'W], 1680 m. The holotype was collected in pine forest (Pinus pseudostrobus) heavily laden with bromeliads; this region lies within the Lower Montane Moist Forest Life Zone of Holdridge (Organization of American States 1962).

Distribution.--Known only from pine and mixed pine and oak forests in highlands immediately east of Tegucigalpa; perhaps occurs throughout the Lower Montane Moist Forest Life Zone community or in high elevation

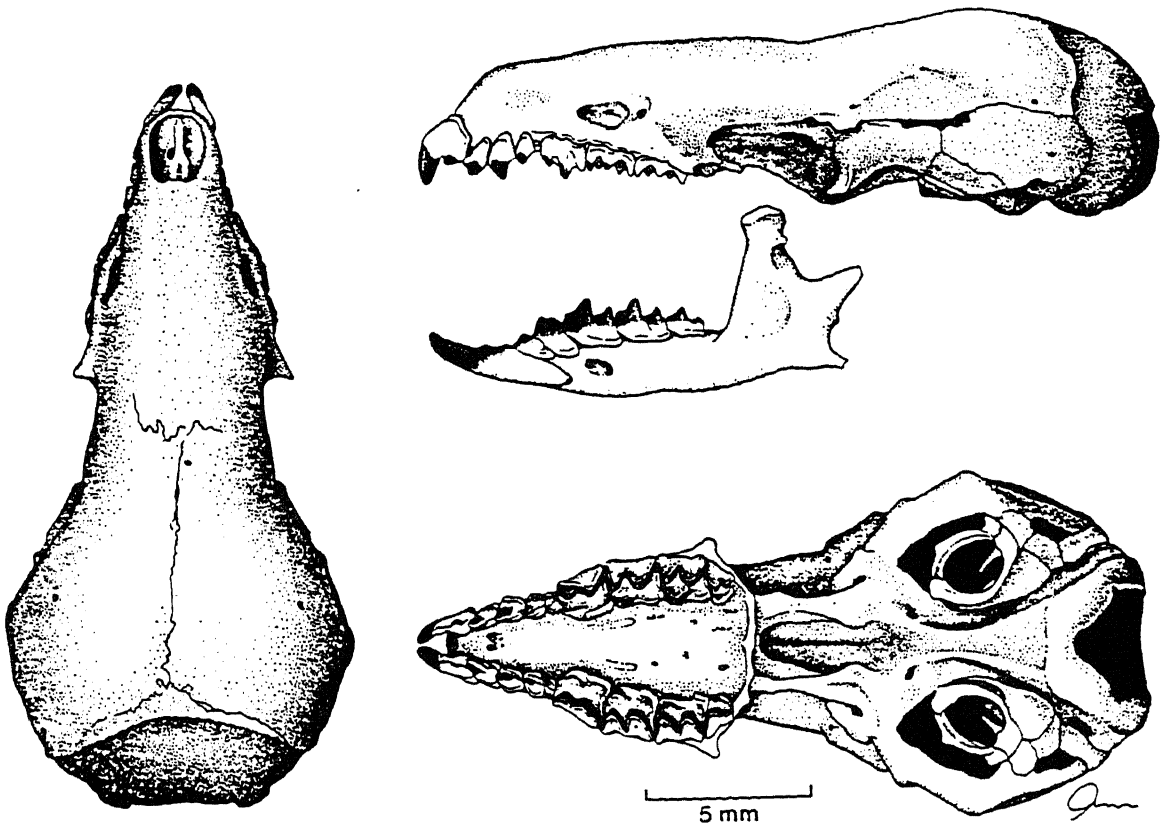

Figure 2. Dorsal and ventral view of the skull and lateral views of the skull and mandible of the holotype of C. hondurensis (KU 106941).

pine forests in Honduras and possibly in neighboring areas of Guatemala, El Salvador, and Nicaragua.

Measurements of Holotype.--Total length, ca. 84; tail, 29; hind foot, 12; ear, 6: condylobasal length, 19.2; palatal length, 8.4; maxillary breadth, 6.0; interorbital breadth, 4.3; maxillary toothrow, 7.1; cranial breadth, 9.2; mandibular toothrow, 5.5 (see Table 1).

Diagnosis.--A smaller species of the genus Cryptotis characterized by its similar dorsal and ventral coloration, a long and tapered tail, a long and narrow snout, a long zygomatic plate, a complex M3, nearly perpendicular conformation of the junction of the the coronoid process with the horizontal ramus, a short and broad articular process, and talonid of m3 with only a single cusp.

Description.--Size small for the genus (Table 1); tail long (ca. 42-53% of head and body length), tapering to a point; front feet and claws normal for genus, not enlarged; viewed ventrally, the snout is long and narrow; when air-dried the pelage of the fluid-preserved holotype is dense and soft, the dorsal guard hairs about 4 to 5 mm long; dorsal fur shows distinct banding, the

Table 1.--Means (± SD) and observed ranges for skin, cranial, and mandibular measurements of Central American Cryptotis used in this study. Sample sizes (in parentheses) may be different for head and body length, tail length, and condylobasal length. The order of measurements of C. hondurensis is the holotype followed by the two paratypes. Missing measurements from the paratypes are represented by x.

Table 1

C. hondurensis (holotype and 2 paratypes)	*C. gracilis* (n = 20)	*C. nigrescens merriami* (n = 13)	*C. parva orophila* (n = 16)
head and body length			
55, 63, 64	73 ± 5 60-79 (n = 18)	69 ± 4 65-76	65 ± 7 58-77 (n = 11)
tail length			
29, 27, 27	34 ± 3 30-41 (n = 18)	29 ± 3 24-33	21 ± 2 17-24 (n = 11)
tail length [as % of head and body length]			
53, 43, 42	48 ± 5 38-58 (n = 18)	42 ± 5 32-50	33 ± 4 29-38 (n = 11)
condylobasal length			
19.2, x, x	19.6 ± 0.5 18.7-20.4	19.4 ± 0.3 18.9-20.0 (n = 11)	17.1 ± 0.3 16.7-17.7 (n = 10)
zygomatic plate length			
2.2, 2.0, 2.1	1.8 ± 0.1 1.5-2.0	2.3 ± 0.2 2.0-2.6	1.5 ± 0.1 1.4-1.8
interorbital breadth			
4.3, 4.5, x	4.7 ± 0.2 4.1-5.2	4.8 ± 0.1 4.5-4.9	4.0 ± 0.1 3.8-4.35
U1-U1 breadth			
2.4, 2.4, x	2.4 ± 0.2 2.0-2.6	2.7 ± 0.1 2.4-2.8	2.4 ± 0.1 2.0-2.5
M2-M2 breadth			
5.4, 5.4, x	5.4 ± 0.3 5.0-5.8	5.9 ± 0.1 5.6-6.2	5.1 ± 0.2 4.9-5.5
palatal length			
8.4, 7.8, x	8.8 ± 0.3 8.3-9.3	8.4 ± 0.2 8.1-8.8	7.2 ± 0.4 6.0-7.8

Table 1 (cont.)

C. hondurensis	C. gracilis	C. nigrescens merriami	C. parva orophila
maxillary toothrow length (U1-M3)			
7.1, 7.1, 7.1	7.6 ± 0.3 7.1-8.0	7.4 ± 0.1 7.1-7.5	6.2 ± 0.2 5.9-6.7
unicuspid toothrow length			
2.6, 2.4, 2.4	2.6 ± 0.1 2.4-2.9	2.5 ± 0.1 2.3-2.6	2.0 ± 0.1 1.8-2.2
posterior width of M1			
1.7, 1.7, 1.9	1.7 ± 0.1 1.6-1.8	1.9 ± 0.1 1.8-2.0	1.6 ± .1 1.6-1.8
mandibular length (inferior sigmoid notch to mental foramen)			
6.1, 5.8, 6.3	6.4 ± 0.2 6.1-6.7	6.6 ± 0.2 6.3-6.8	5.4 ± 0.2 4.8-5.8
coronoid process height			
4.8, 4.4, 4.6	4.1 ± 0.2 3.7-4.4	5.1 ± 0.2 4.8-5.3	4.1 ± 0.2 3.7-4.3
articular condyle height			
3.6, 3.6, 3.8	3.7 ± 0.2 3.3-4.0	3.8 ± 0.2 3.6-4.3	3.4 ± 0.1 3.2-3.7
distance from articular condyle to m3			
4.3, 4.3, 4.4	5.1 ± 0.2 4.8-5.3	4.7 ± 0.1 4.5-4.9	4.1 ± 0.1 4.0-4.3
articular condyle breadth			
3.0, 2.8, 2,8	3.0 ± 0.1 2.7-3.1	3.1 ± 0.1 3.0-3.2	2.6 ± 0.1 2.4-2.7
mandibular toothrow (p3-m3) length			
5.5, 5.3, 5.7	6.0 ± 0.2 5.6-6.3	5.7 ± 0.1 5.4-5.9	4.9 ± 0.2 4.7-5.3
m1 length			
1.7, 1.7, 1.7	1.7 ± 0.1 1.5-1.8	1.8 ± 0.2 1.7-1.9	1.5 ± 0.1 1.3-1.6

proximal 75% of the guard hairs is pale gray in color, whereas the distal 25% is close to Prout's Brown; venter appears somewhat paler than dorsum. The overall brownish coloration of the specimen may be due to fading or bleaching. This color resembles some older, fluid-preserved specimens of C. gracilis, yet C. gracilis preserved as dried study skins are Fuscous to Chaetura Black.

Rostrum long, of medium breadth relative to other Cryptotis (Fig. 2); interorbital constriction of medium breadth; braincase low, flat; zygomatic plate long, anterior border aligned with mesostyle-metastyle valley of M1, posterior border aligned with posterior base of maxillary process and middle of M3; upper toothrow may be uncrowded, U4 aligned with toothrow and clearly visible in labial view (holotype--Fig. 5B) or crowded, U4 displaced medially and not clearly visible in labial view (both paratypes); P4, M1, M2 slightly recessed on posterior border; M3 with paracrista, precentrocrista, and short postcentrocrista, as well as well developed protocone, paracone, and metacone; dentition not particularly bulbous.

Mandible short, moderately broad for the genus (Fig. 2); coronoid process joins horizontal ramus at nearly a right angle; distance between coronoid process and

posterior border of m3 is short; viewed posteriorly, articular process is short and narrow, with a broad ventral articular facet (Fig. 6B); lower sigmoid notch shallow; upper sigmoid notch rounded; posterior border of lower incisor extends posterior to the cusps of p4; talonid of m3 consists of hypoconid only.

Comparisons.--Cryptotis hondurensis resembles C. gracilis in its long tail, the complexity of the cusps of M3, and in some general external and cranial features, which account for its previous allocation to the latter species. However, it is much closer in many other features to C. nigrescens merriami, to which it may be most closely related phylogenetically. It differs from C. gracilis, C. nigrescens merriami, and C. parva orophila in the following:

Cryptotis gracilis (Figs. 3, 5A, 6A): C. hondurensis has shorter (4-5 mm vs. 6-7 mm), less woolly dorsal pelage; a shorter, broader rostrum that is not as highly arched; narrower braincase; narrower interorbital constriction; longer zygomatic plate; relatively shorter maxillary toothrow; P4 almost quadrate; M1 shorter and broader; paracone and metacone of M3 closer together; coronoid process absolutely higher, joining horizontal ramus at nearly a right angle; shorter distance between

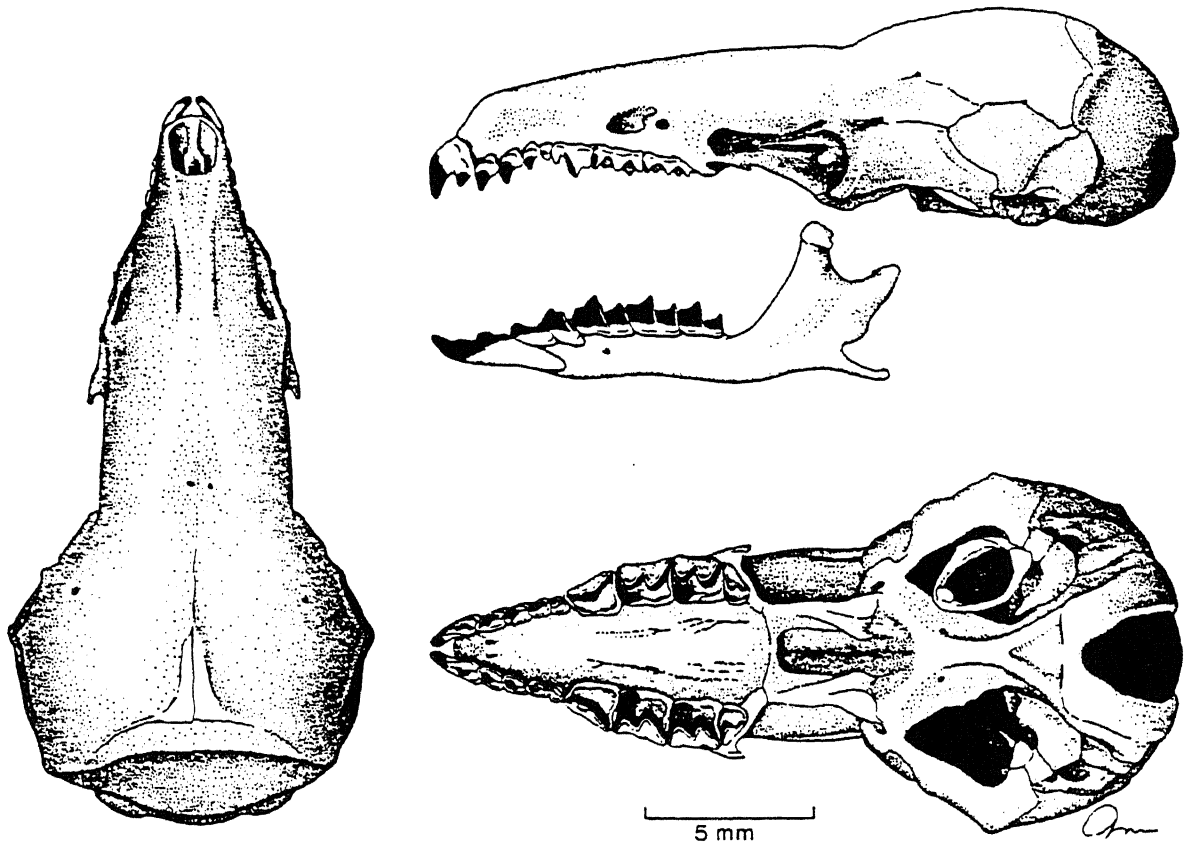

Figure 3. Dorsal and ventral view of the skull and lateral views of the skull and mandible of C. gracilis (LSU 12659).

coronoid process and m3; shorter mandibular toothrow; shorter, broader articular process, with much broader ventral articulating surface; shallower lower sigmoid notch; posterior margin of lower incisor extends posterior to cusps of p4; broader and more massive m1 and m2; talonid of m3 consists of only hypoconid.

Cryptotis parva orophila: C. hondurensis is larger and has a longer tail relative to body; longer (4-5 mm vs. 3-4 mm), silkier dorsal pelage; longer, narrower rostrum; lower, flatter braincase; P4, M1, M2 not as deeply recessed posteriorly; M3 with paracrista, precentrocrista, postcentrocrista, and well developed paracone and metacone; narrower articular process of mandible, with much broader ventral articulating surface.

Cryptotis nigrescens merriami (Figs. 4, 5C, 6C): C. hondurensis has a longer, narrower tail, tapering to a point at its tip rather than being thick and rounded as in C. nigrescens merriami; relatively longer, narrower rostrum; much narrower palate; lower, flatter braincase; less massive upper and lower molars and upper unicuspids; M3 with paracrista, precentrocrista, postcentrocrista, and well developed paracone and metacone; teeth not bulbous; smaller and narrower

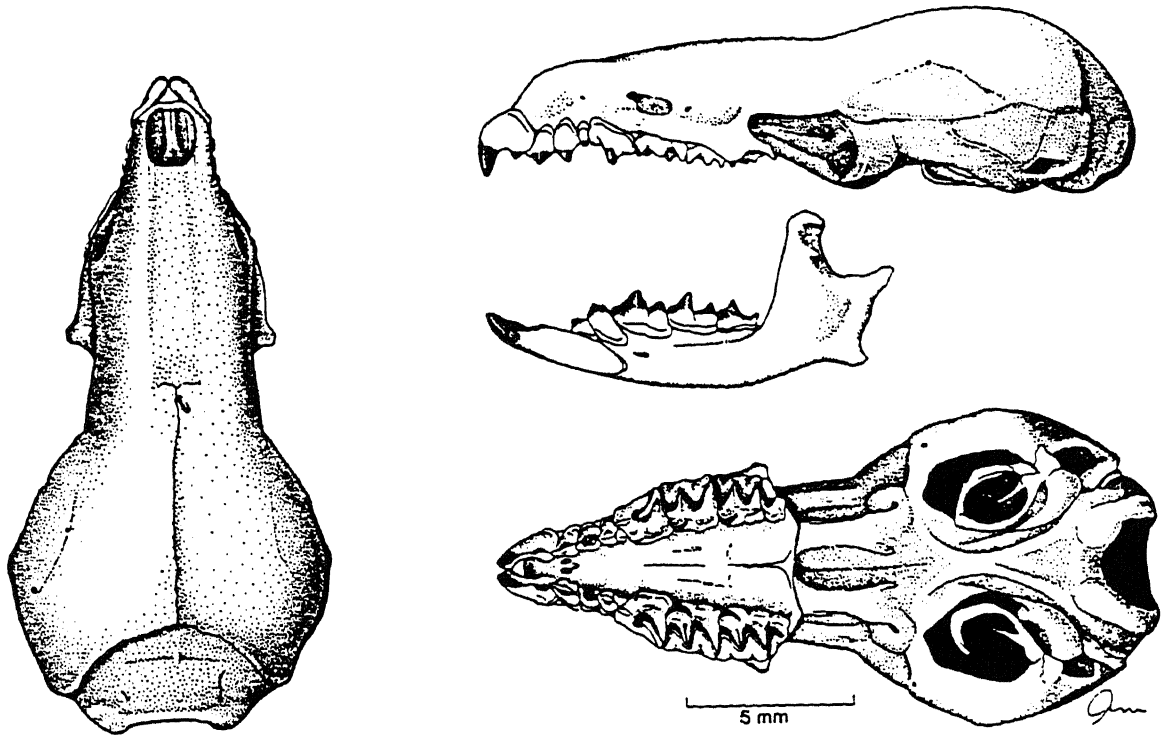

Figure 4. Dorsal and ventral views of the skull and lateral views of the skull and mandible of C. nigrescens merriami (MVZ 130335).

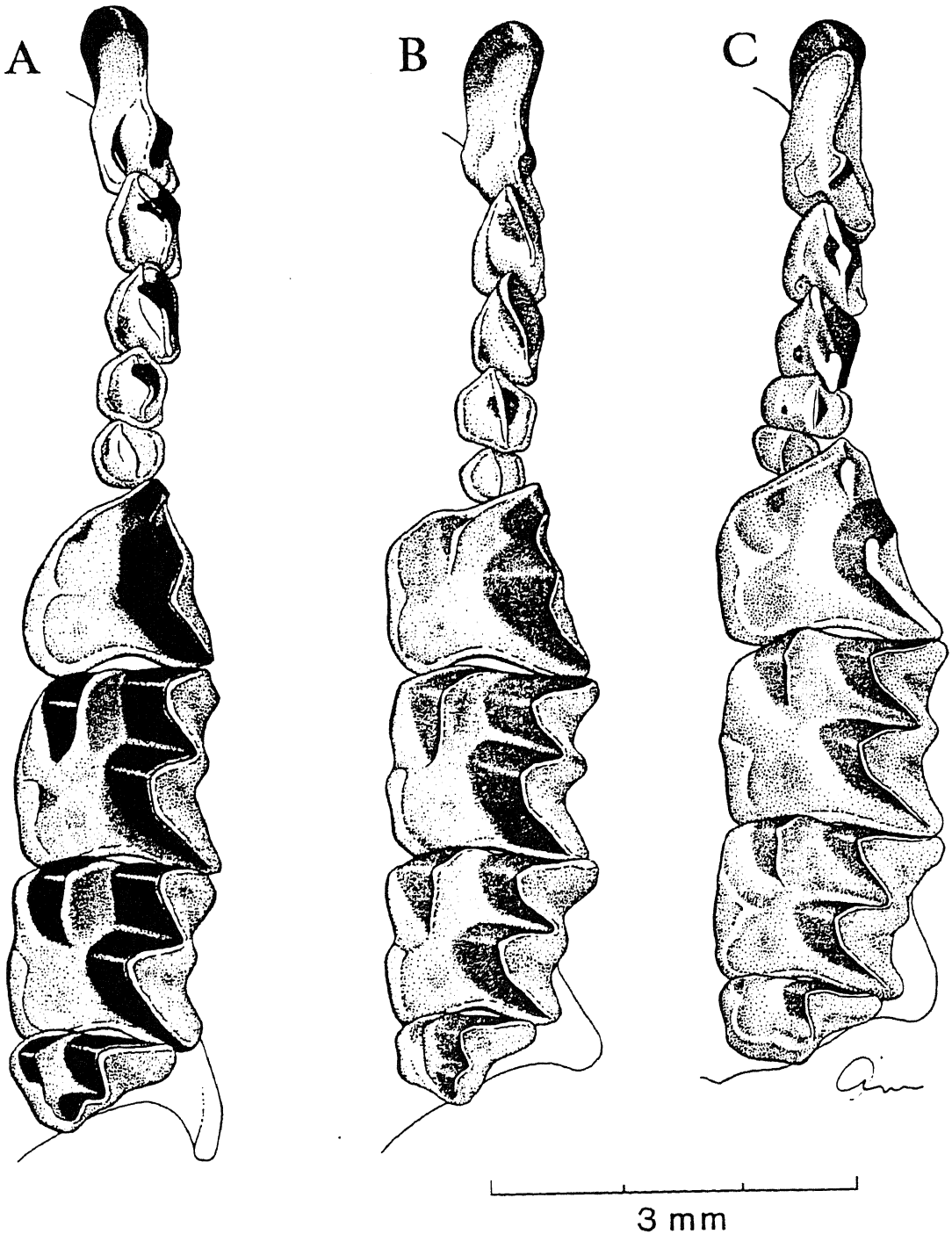

Figure 5. Left maxillary toothrows of C. gracilis (A), C. hondurensis (B), and C. nigrescens merriami (C).

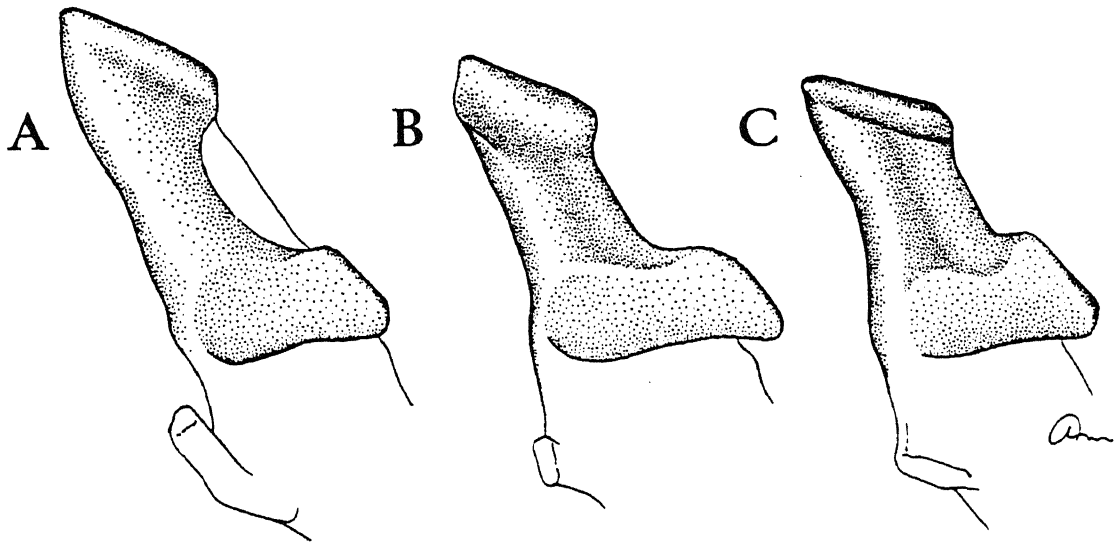

Figure 6. Left mandibular articular condyles of C. gracilis (A), C. hondurensis (B), and C. nigrescens merriami (C).

articular process of mandible.

Etymology.--The specific epithet hondurensis is derived from Honduras, the country of origin of the holotype and both paratypes.

Multivariate analyses

Discriminant function analysis yielded a numerical model that required four measurements to discriminate among the three species: palatal length, coronoid process height, distance from articular condyle to posterior of m3, and zygomatic plate breadth. All specimens of C. gracilis, C. nigrescens, and C. parva were correctly classified into their predetermined groups. The holotype and paratype of C. hondurensis are clearly distinct from C. gracilis and are closest to C. nigrescens merriami in general cranial shape and size, as can be seen in a plot of specimens on canonical axes 1 and 2 (Fig. 7).

Principal components analysis reveals clear distinctions among the four taxa, separating without overlap all specimens of C. gracilis, C. nigrescens, and C. parva, and showing C. hondurensis intermediate amongst them on factor axes 1 and 2 (Fig. 8). In this model, Factor 1 is clearly a size axis and Factor 2 is a shape axis contrasting a group of variables representing

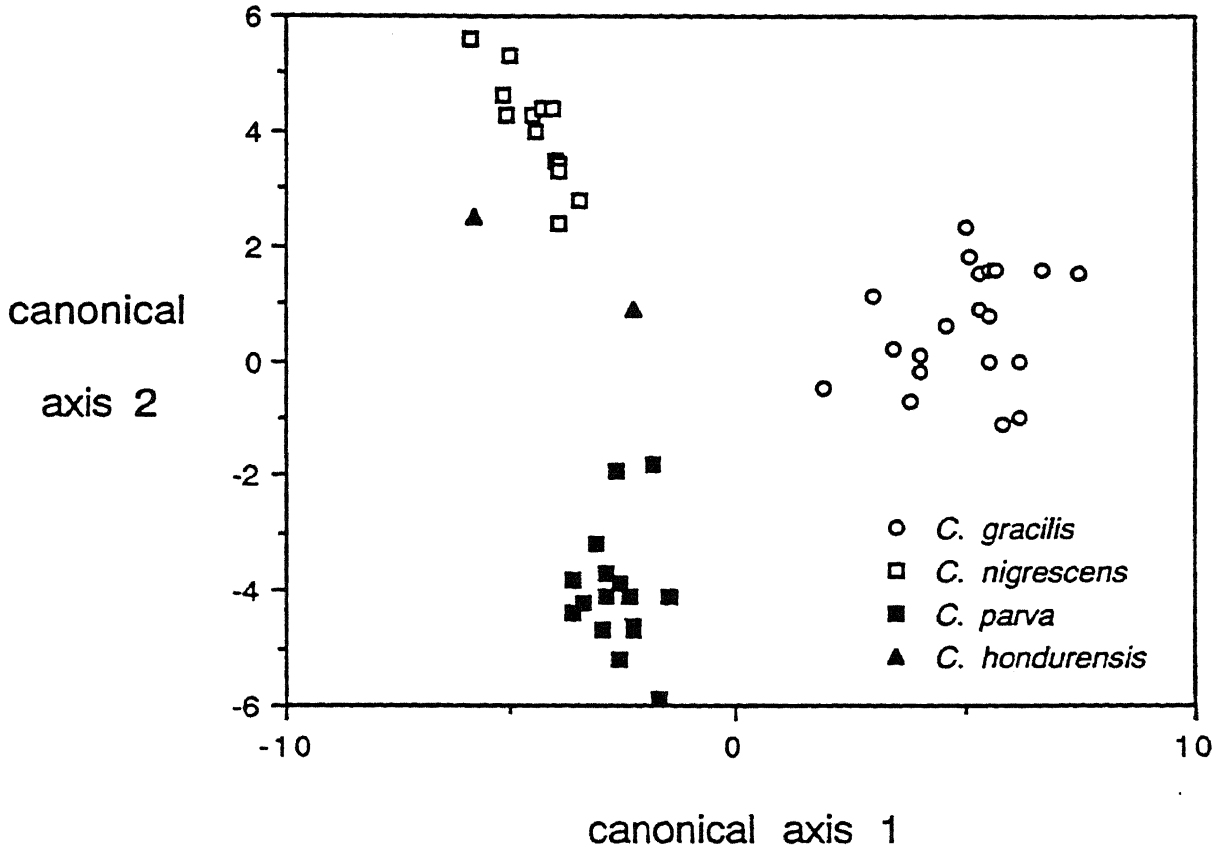

Figure 7. Plot of specimens of C. gracilis, C. nigrescens merriami, and C. parva orophila and the holotype and one paratype of C. hondurensis on canonical axes 1 and 2.

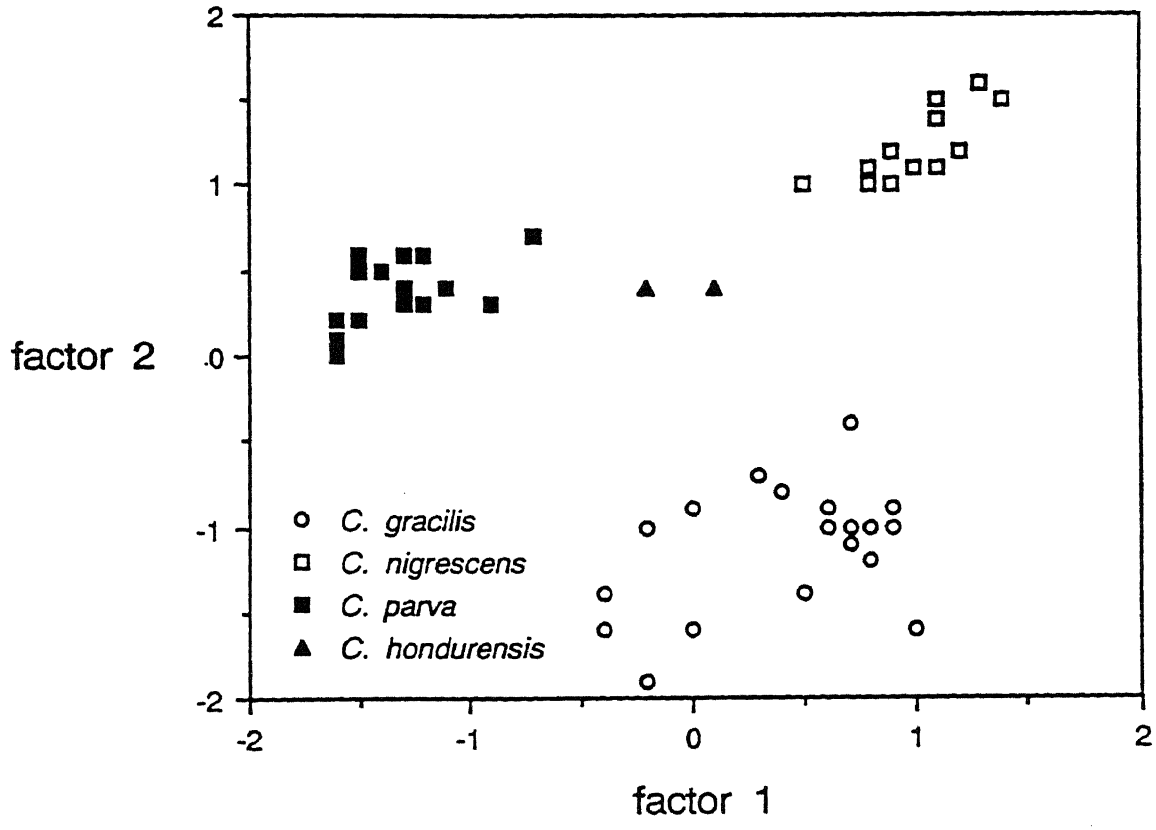

Figure 8. Plot of specimens of C. gracilis, C. nigrescens merriami, and C. parva orophila and the holotype and one paratype of C. hondurensis on principal components factor axes 1 and 2.

mandibular height and palatal width (coronoid process height, posterior width of M1, U1-U1 breadth, zygomatic plate breadth, and M2-M2 breadth) with a second group of variables representing mandibular and palatal lengths (articular condyle to m3 distance, palatal length, unicuspid toothrow, mandibular toothrow, and maxillary toothrow).

Discussion

Choate (1970:284) first noted some of the differences between the Honduran specimen and Costa Rican C. gracilis: "the specimen from Honduras differs from typical Costa Rican individuals in being slightly smaller, both externally and cranially, and in having only one cusp (the hypoconid) as opposed to both hypoconid and entoconid on the talonid of m3." Although the crania of C. hondurensis and C. gracilis appear similar in general aspect, important differences exist, particularly in the shape of the rostrum and the breadth of the zygomatic plate. In addition, the mandibles of the two species are quite distinct (Figs. 2, 3). Cryptotis gracilis has a long, narrow, mandibular ramus with small teeth and an uncrowded toothrow. The coronoid process has a wide base that attaches to the ramus at a low angle. The shape and angle of the

coronoid process in C. gracilis is unlike any Recent or fossil Holarctic soricid I have studied and instead allies C. gracilis with certain Central American and South American species. In contrast, C. hondurensis has a mandible more typical of the family: short and broad, with the coronoid process joined to the horizontal ramus at a nearly right angle. The mandibular articular process of C. hondurensis is similar to that of C. nigrescens, but the lower articulation is relatively much broader in C. hondurensis than in other species of Cryptotis I have studied.

Among species of Cryptotis the M3 is highly variable in size and coronal complexity. Choate (1970) indicated that, in the primitive condition, the tooth is relatively large with paracrista, paracone, precentrocrista, postcentrocrista, metacone, and metacrista. In more specialized grades, M3 becomes successively shortened posteriorly, with resulting diminution and loss of the more posterior and lingual structures (Choate 1970). If this character polarity is true, then the M3 of C. hondurensis, like that of C. gracilis, is rather primitive for the genus. Cryptotis hondurensis possesses both paracone and metacone on M3 but, unlike C. gracilis, these structures are close together and the mesostyle does not extend very far

labially (Fig. 5A, B).

Using keys to North and Middle American Cryptotis provided by Choate (1970) and Hall (1981), C. hondurensis would be identified as C. gracilis in couplet 2'. However, the two species can be separated readily on the basis of the contrasting characters described above.

The Honduran specimen referred to C. gracilis by Choate (1970) represented the only known example of C. gracilis from north of Costa Rica. Recognition of this animal as a distinct species restricts the known range of C. gracilis to the Talamancan and Tilarán highlands of Costa Rica and the adjacent Chiriquí highlands of extreme western Panama.

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Woodman, N., and R. M. Timm. submitted. Morphological variation and speciation in the Cryptotis gracilis species complex (Insectivora: Soricidae) in Costa Rica and Panama. Journal of Mammalogy.

Specimens Examined

Cryptotis gracilis (20).--COSTA RICA: CARTAGO: Volcán Irazú, Finca Coliblanco, 2350 m (2 UMMZ); Volcán Irazú, .25 mi N of San Juan Chicoa, 2860 m (1 UMMZ); Volcán Irazú, 2500 m (1 KU); Volcán Turrialba, Hacienda El Retiro, 2590 m (4 UMMZ). SAN JOSE: Cerro Chirripó, Headwaters of Río Talari, 11,600 ft (4 LSU); Cerro de La Muerte, Hotel Georgina, 3100 m (1 USNM); La Piedra, ca. 4 mi SW Cerro Chirripó, 10,500 ft (4 LSU); Las Vueltas, 8000 ft (1 UMMZ). PANAMA: BOCAS DEL TORO: Cerro Fabrega, 8400 ft (1 USNM). CHIRIQUI: Cerro Punta, Boquete Trail, 7600 ft (1 USNM).

C. hondurensis (3).--HONDURAS: FRANCISCO MORAZAN: Cerro Uyuca (1 KU - holotype); near San Juancito mines, 1700 m (1 FMNH); La Rosario, San Juancito, La Tigra National Park (1 UNAH).

C. nigrescens merriami (13).--EL SALVADOR: MORAZAN: Mount Cacaguatique, 3800-4700 ft (2 MVZ). SAN MIGUEL: Mount Cacaguatique, 3500-4000 ft (7 MVZ, 2 UMMZ). GUATEMALA: ALTA VERAPAZ: Tucuru, Hacienda Concepción, 1100 m (1 UMMZ). HUEHUETENANGO: Barillas, Hacienda Santa Gregoria (1 UMMZ).

C. parva orophila (16).--COSTA RICA: ALAJUELA: Zarcero, 6000 ft 1 FMNH); CARTAGO: Cartago (2 UMMZ); Cerro Tablazo, 1983 m (1 USNM); La Estrella (1 AMNH). HEREDIA: Barva, San José de la Montaña, Paso Llano, 1800 m (3 KU); Barva, San Miguel de la Montaña, 1690-1700 m (3 KU). SAN JOSE: 10 mi S. of Cartago, El Muñeco, 3800 ft (1 UMMZ); San Rafael de Montes de Oca, 4300 ft (1 KU); Santa Ana (1 LSU). NICARAGUA: JINOTEGA: 12 km S. of Jinotega, 1400 m (1 KU). MATAGALPA: 9 mi N. of Matagalpa, Santa Maria de Ostuma, 1300 m (1 UMMZ).

MORPHOLOGICAL VARIATION AND SPECIATION IN THE *CRYPTOTIS GRACILIS* SPECIES COMPLEX (INSECTIVORA: SORICIDAE) IN COSTA RICA AND PANAMA

Small-eared shrews of the genus *Cryptotis* are poorly known despite their wide distribution in North America, Central America, and northern South America. These shrews are found in extreme southern Ontario, across much of the eastern and midwestern United States, through portions of Mexico and Central America, and in the northern Andean highlands. Most of our current information about *Cryptotis* comes from studies of one species, *C. parva*, in the United States (e.g., Whitaker, 1974), yet the genus attains its greatest diversity in the Central American tropics, where it remains mostly unstudied.

In their synopsis of North American mammals, Hall and Kelson (1959) recognized 25 species in the genus *Cryptotis* in Mexico and Central America. Choate (1970), in his landmark monograph on the Middle American *Cryptotis*, recognized eight species in this same region, and his taxonomy has been followed by subsequent authors, including Hall (1981).

Among the least known of the Central American species of small-eared shrews is the high elevation species,

Cryptotis gracilis. Miller (1911) first recognized C. gracilis as a distinct species based on a single specimen from near Pico Blanco, Limón Province, Costa Rica. Little subsequent work was done with the species, in part because few specimens were available. Choate (1970) provided the only comprehensive treatment of the taxonomy and distribution of C. gracilis. At that time C. gracilis was thought to occur from the highlands of southern Honduras to the Chiriquí Cordillera in western Panama. In Honduras the species was represented by a single specimen from Cerro Uyuca, Francisco Morazán Department, and a large gap existed in the known range between Honduras and the Central Cordillera in Costa Rica (Choate, 1970).

Recent collecting has made available for study additional specimens of C. gracilis, many from previously uncollected areas. These new specimens now permit a review of geographic variation within the species. As a result, we (Woodman and Timm, 1992) recently recognized the specimen from Cerro Uyuca, and additional specimens from Francisco Morazán Department, Honduras, as a distinct and unrelated species, C. hondurensis, thus restricting the range of C. gracilis to the highlands of central and southern Costa Rica and western Panama. Within this range in Costa Rica and

Paṇama, specimens previously identified as C. gracilis are known from four highland areas isolated by intervening lowlands: 1) Monteverde in the Tilarán Cordillera, 2) Volcán Barva, 3) the Volcán Irazú/Volcán Turrialba complex in the Central Cordillera, and 4) the Talamancan Cordillera of southern Costa Rica and the adjoining Chiriquí Cordillera of westernmost Panama (Fig. 9). Further study of specimens from these regions indicates that morphological differentiation has occurred to the degree that four distinct species are now recognized: C. gracilis, C. jacksoni [originally described as a distinct species, but considered equivalent to C. gracilis by Choate (1970) and Hall (1981)], and two species new to science.

Systematics of the genus Cryptotis are not resolved as yet, but studies are continuing and will be addressed at a later date. For the purposes of this paper the Costa Rican and Panamanian taxa previously called C. gracilis are referred to informally as members of the "C. gracilis group". While preliminary evidence suggests that this is a monophyletic group, a comprehensive phylogenetic study is not yet complete.

The purposes of this paper are to: 1) redescribe and illustrate the two previously described species in the C. gracilis group; 2) provide descriptions and

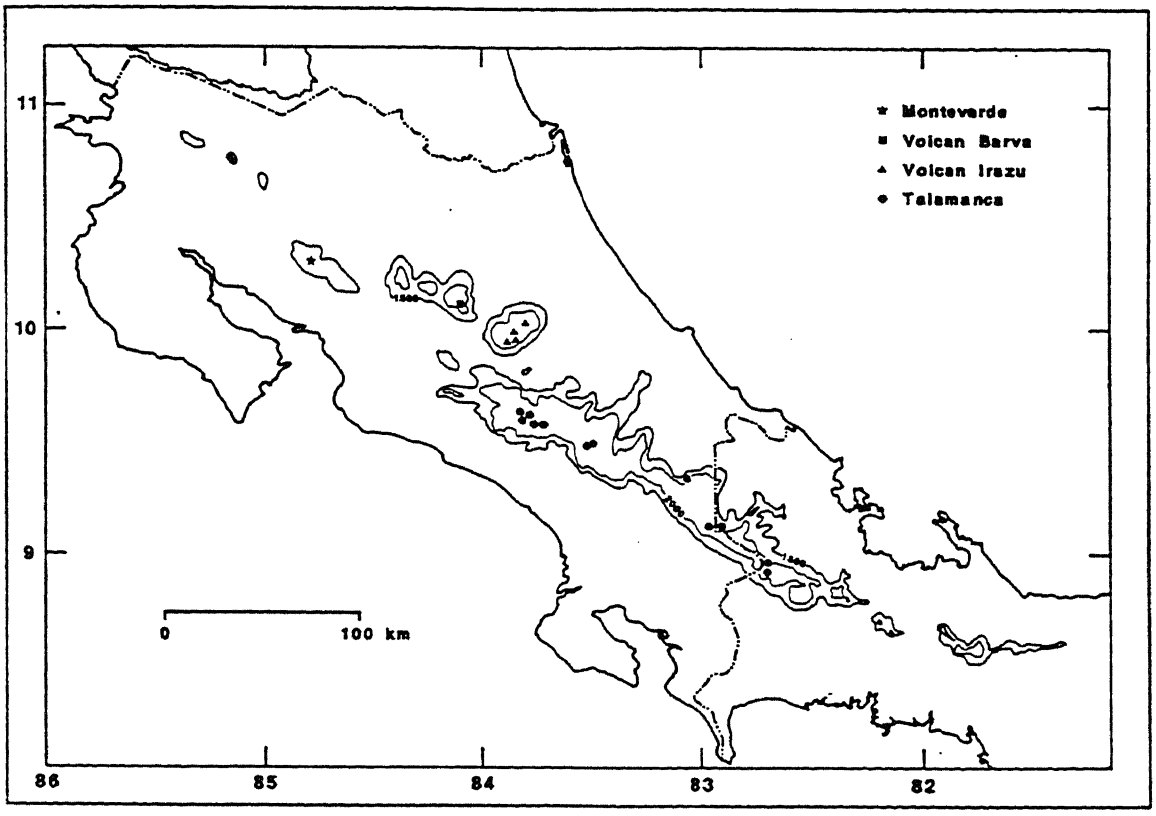


Figure 9. Map of Costa Rica and westernmost Panama showing the distribution of members of the C. gracilis group. Contours are shown for 1500 m and 2000 m elevations.

illustrations of two species new to science; 3) provide a key to all of the known species in Costa Rica; 4) review the available information on reproduction, elevational distribution, and habitat for the members of this complex.

Methods

Cranial and mandibular measurements were all taken to the nearest 0.1 mm using either an ocular micrometer in a binocular microscope or a hand-held dial caliper. Skin measurements are those recorded by the collector, except for head and body length, which we calculated by subtracting the recorded tail length from the total length. All measurements are in millimeters. Terminology of dental characteristics follows Choate (1970). We also follow Choate (1970) in referring to the upper dentition between the incisor and P4 as unicuspids, abbreviated U1, U2, etc. The following measurements were used in our analyses, and each is referred to using the abbreviation in parentheses following the measurement (Fig. 10): head and body length (HB); tail length (TL); condylobasal length (CBL), not including the upper incisors; cranial breadth (CB); breadth of zygomatic plate (ZP); interorbital breadth (IO); breadth of palate across first unicuspids

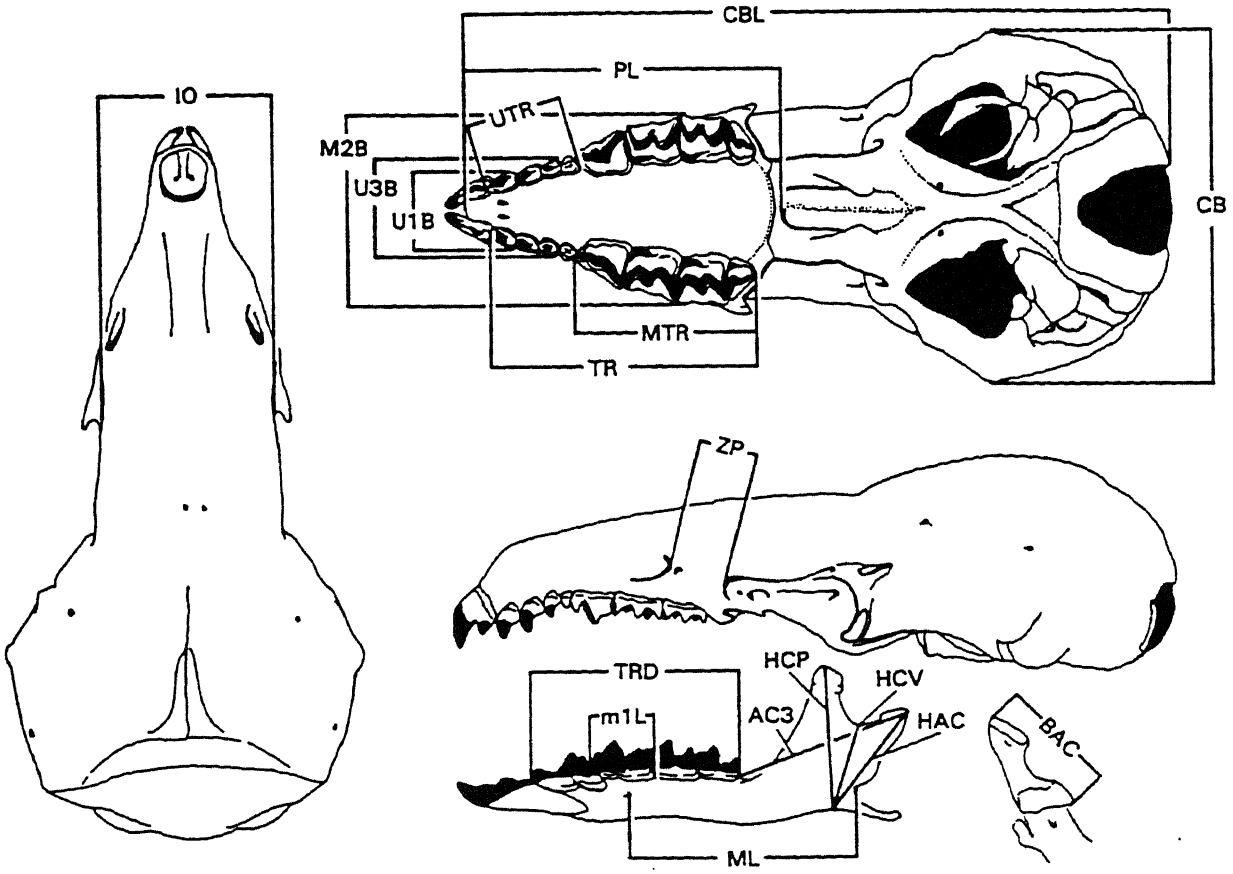


Figure 10. Diagram showing the measurements used in this study. Abbreviations are explained in the text.

(U1B); breadth of palate across third unicuspids (U3B); breadth of palate across second molars (M2B); palatal length (PL); upper toothrow length, U1 to M3, parallel to the long axis of the skull (TR); unicuspid toothrow length, parallel to the unicuspid toothrow (UTR); molariform toothrow, P4 to M3, parallel to long axis of the skull (MTR); posterior width of M1, across hypocone and metastyle (WM1); mandibular length, from deepest point of inferior sigmoid notch to posterior edge of mental foramen (ML); height of coronoid process (HCP); height of coronoid valley (HCV); height of articular condyle (HAC); breadth of articular condyle (BAC); distance from articular condyle to posterior edge of m3 (AC3); lower toothrow length (TRD); length of m1 (m1L). All capitalized color names follow Ridgeway (1912). Localities and elevations we report are taken directly from specimen tags and represent the descriptions of the original collectors. We provide corrections and additions in brackets. We do not convert distances measured in miles or elevations measured in feet to the metric system to avoid inferring a level of accuracy greater than that originally recorded by the collector. We use Talamanca to refer to the Talamancan and Chiriquí highlands, and Irazú to refer to the Volcán Irazú/Volcán Turrialba highland complex.

Analyses of variance (ANOVA) and multivariate analyses were carried out using BMDP on the University of Kansas Academic Computing Services' IBM 3031AP processor running a VM/CMS computer system. Regression statistics were calculated using Minitab version 6.2 for IBM compatible personal computers.

Males and females of Cryptotis are generally difficult to distinguish, and few tests for sexual dimorphism within the genus have been carried out. Choate (1970) found length of maxillary toothrow was the only measurement that was significantly different between the sexes in his morphometric examination of C. mexicana. Because there were no localities with large samples of both males and females, we tested for sexual variation within C. gracilis by carrying out a two-way ANOVA on each of 20 variables (HB, TL, CBL, ZP, PO, U1B, M2B, PL, TR, UTR, MTR, WM1, ML, HCP, HCV, HAC, BAC, TRD, Lm1, AC3) using 25 specimens from three localities within Talamanca. Both sex and locality were used as the factors in order to separate the effects of sexual dimorphism and geographic variation. Only specimens from Talamanca were used in order to avoid the possibility of confounding effects of variation among the four geographically isolated regions. Within Talamanca we used only specimens from those localities

with at least three males and three females.

Sexual dimorphism was further examined by attempting to separate 13 males and 16 females from throughout Talamanca using discriminant function analyses on 8 variables (CBL, ZP, PO, M2B, TRL, ML, HCP, AC3). When the first test, using a protected F-to-enter (α = 0.05/9 comparisons = 0.0056), failed to enter any variables, a second test was run using an artificially low F-to-enter (F = 3.00; α = 0.095). In order to test whether other variables might be useful in distinguishing between the sexes, a 16 variable model (CBL, ZP, PO, U1B, M2B, PL, TR, UTR, WM1, ML, HCP, HAC, BAC, TRD, m1L, AC3 - Table 2) was tried, also using the artificially low F-to-enter. Because of the lack of strong evidence of sexual dimorphism in size or shape (see Results, below), males, females, and specimens of unknown sex were used together in all subsequent analyses.

Principal components analysis (PCA) was carried out using 17 variables (HB, TL, ZB, PO, U1B, M2B, PL, TR, UT, WM, LM, HCP, AM3, HAC, BAC, TLD, m1L) on 47 specimens, 32 from Talamanca, 13 from Irazú, and the individual specimens from Volcán Barva and Monteverde.

Because specimens from Irazú cluster together on plots of factor scores from the principal components analysis (see Results, below), discriminant function

analyses (DFA) were used in an attempt to separate them from specimens from Talamanca. Discriminant function analyses were performed using 9 variables (HB, TL, PO, M2B, PL, HCP, HAC, AC3, BAC). The single specimens from Monteverde and Volcán Barva were added to the discriminant function model as unknowns to see where they would plot in relation to the two known groups. A protected F-to-enter (α = 0.05/9 comparisons = 0.0056) was used for this analysis because of the multiple comparisons among groups.

The range of the C. gracilis group follows the line of the Central American cordillera, which runs roughly northwest to southeast in Costa Rica and western Panama (Fig. 9). To test for geographic variation through the range of this group, we first ran a PCA on latitude and longitude for all shrew capture sites. Because these sites fall nearly in a line, PCA factor 1 provides a single score for each capture site representing both latitude and longitude. This score was used to represent each geographic locality in subsequent analyses. We refer to it in subsequent analyses as "location".

To test whether the morphological variation we saw among specimens from the four geographic regions could be explained as a result of clinal trends size and

shape, we regressed scores on PCA factor 1 and 2 from the analysis of morphological variation, and several individual variables (HB, TL, CBL, PL, U1B, M2B, and LM), separately on location and elevation for specimens of C. gracilis from Talamanca. Specimens from Talamanca were used to generate the regressions because they represented the largest number of measurable individuals from a single geographic region. We then overlaid specimens from the other three geographic areas on the regressions generated by the Talamanca group to see where they would plot relative to the regression lines.

We tested for elevational clines in Cryptotis from Irazú by regressing on elevation the factor scores and variables used for testing for geographic and elevational variation in Talamancan shrews.

Specimens from the following institutions were used in this study: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio); University of Kansas Museum of Natural History, Lawrence (KU); Los Angeles County Museum, Los Angeles (LACM); Louisiana State University, Baton Rouge (LSU); James Ford Bell Museum of Natural

History, University of Minnesota, Minneapolis (MMNH); Museo Nacional de Costa Rica, San José (MNCR - collections have since been transferred INBio); Museum of Southwestern Biology, Albuquerque (MSB); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); U.S. National Museum, Washington (USNM); University of Michigan Museum of Zoology, Ann Arbor (UMMZ).

Results

Two-way ANOVAs carried out to test for sexual variation among C. gracilis from Talamanca indicated a lack of sexual dimorphism at $p > 0.30$ for most variables. Only two of the twenty variables tested had lower probabilies: HB ($F = 2.64$, $p = 0.1204$) was not statistically different between males and females, but also did not suggest great similarity of means; ZP ($F = 4.91$, $p = 0.0390$) was statistically different between sexes. In contrast, 12 of 20 variables indicated significant ($p < 0.0500$; HB, PO, U1B, M2B, PL, UTR, WM1) or nearly significant ($0.0504 < p < 0.0740$; CBL, TRL, BAC, MTR, m1L) differences among geographic localities within the Talamancan Highlands. ML ($F = 1.77$, $p = 0.1978$) and HCP ($F = 2.24$, $p = 0.1339$) had intermediate probabilities. Six variables showed no indication of variation among the three localities ($p > 0.20$; TL, ZP,

HCV, HAC, TRD, AC3). Both HB ($F = 3.77$, $p = 0.418$) and CBL ($F = 3.27$, $p = 0.0604$) had significant or nearly significant interaction terms, suggesting that male and female variation were not following the same pattern among localities.

In the first DFA for sexual dimorphism using an 8 variable model with a protected F-to-enter, none of the variables showed sufficient variation between sexes to produce an F value larger than the F-to-enter, and no variables were entered. In both the 8-variable and subsequent 16-variable tests using an artifically low F-to-enter, only a single variable, ZP, showed sufficient difference between the sexes to be entered. Only 61.5% of males and 62.5% of females were correctly classified by a jackknifed classification in these two models. Mean ZP is slightly larger in females than in males (1.79 vs. 1.70, respectively; $F = 3.22$, $p = 0.084$).

On a plot of factor 1 scores vs. factor 2 scores from the PCA (Fig. 11), specimens from Irazú tend to cluster together in the lower half of the figure. All variables weighted rather evenly on the first factor axis, indicating that it is a fair measure of overall size. The second axis is a contrast between a combination of TL and AC3 vs. HB and M2B.

A plot of individual specimen scores on the canonical

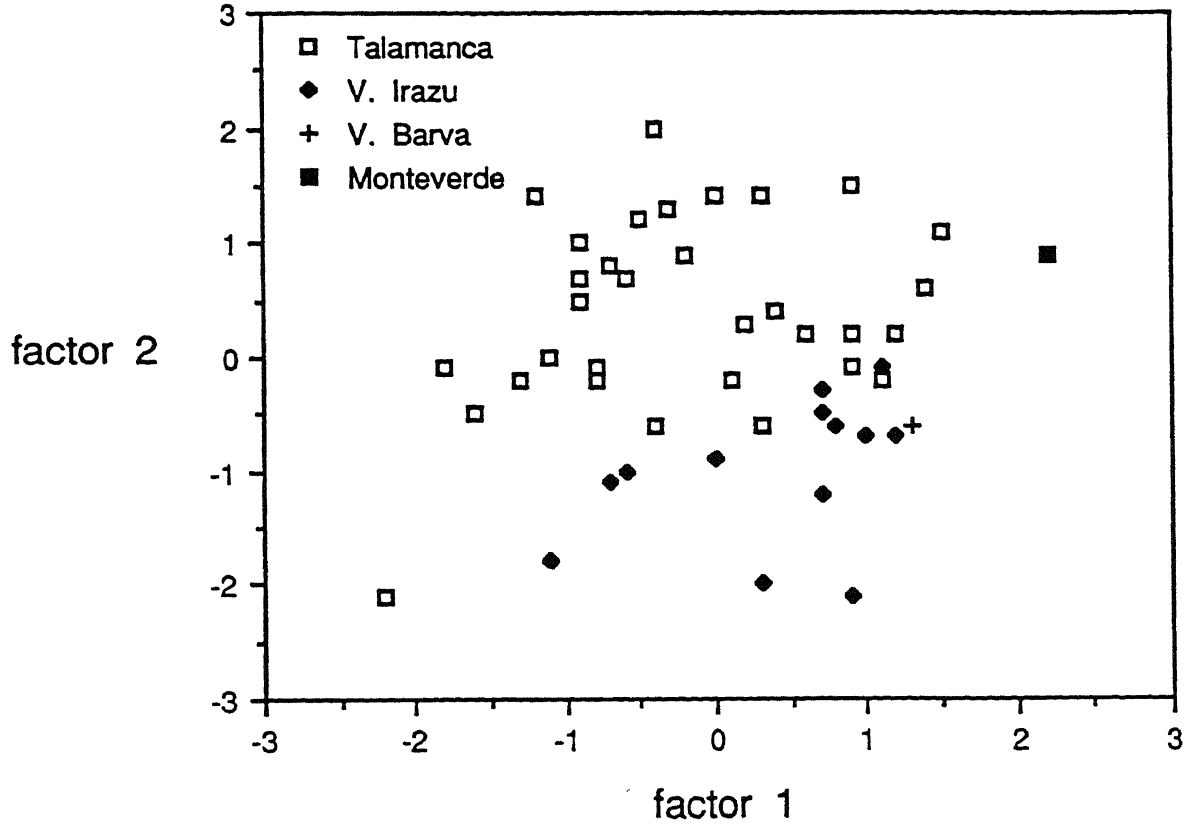


Figure 11. Plot of specimens of the C. gracilis complex on PCA factor axes 1 and 2.

axis from the DFA used to separate specimens from Irazú and Talamanca is shown in Figure 12. The DFA model utilized three variables (M2B, ACB, TL). There was no overlap between specimens from Irazú, on the left side of the plot, and specimens from Talamanca, to the right. However, four specimens from Talamanca plotted to the left of the zero point, which usually indicates the separation between two groups, and two specimens from Talamanca were misclassified as being from Irazú. The two single specimens from Volcán Barva and Monteverde were included in the DFA as unknowns to see where they would plot.

Factor 1 in the PCA of morphological variation among the four groups represents overall size of the specimens. The regression of factor 1 on location is not statistically different from zero (Fig. 13a; $p = 0.460$, $R = 1.8\%$), indicating that there is no clinal increase in size within the Talamancan Highlands. While specimens from Irazú and Volcán Barva tend to be larger, they are not easily separated from the Talamancan shrews on size alone. This is not true, however, for the individual from Monteverde, which is clearly larger overall than any other specimen. Regression of factor 1 on elevation is not statistically significant either for shrews from Talamanca (Fig. 13b; $p = 0.327$, $R = 3.2\%$),

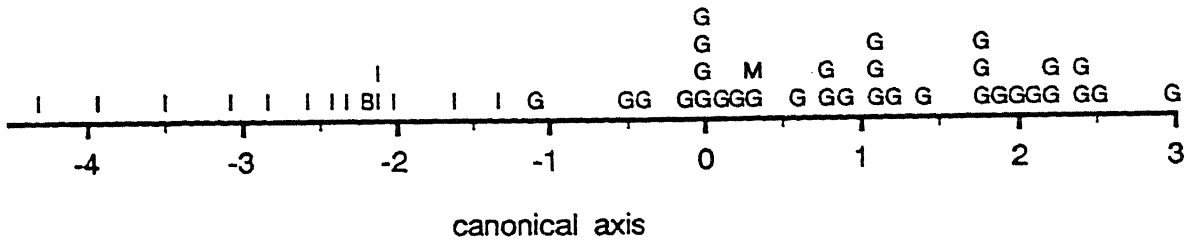
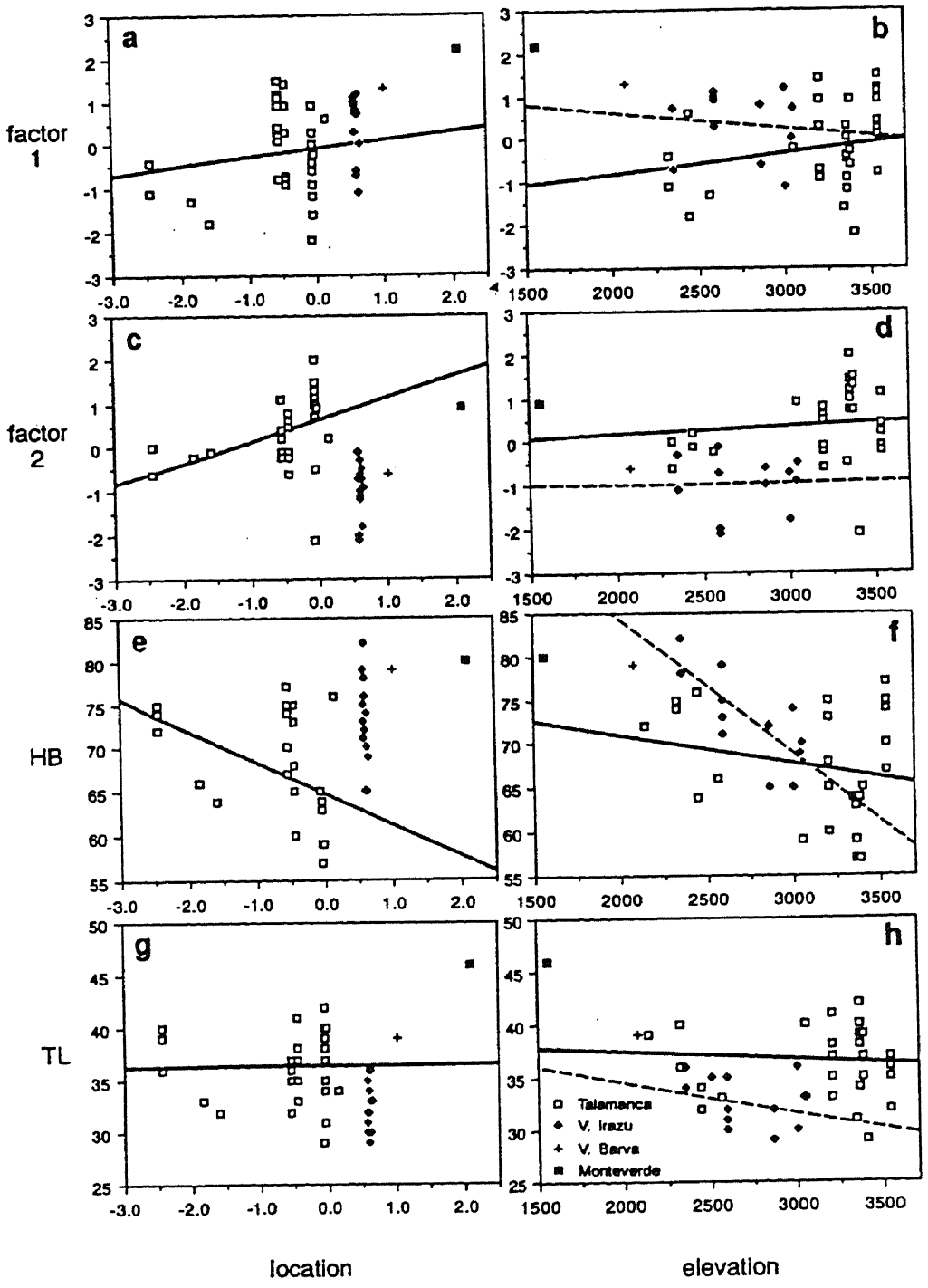
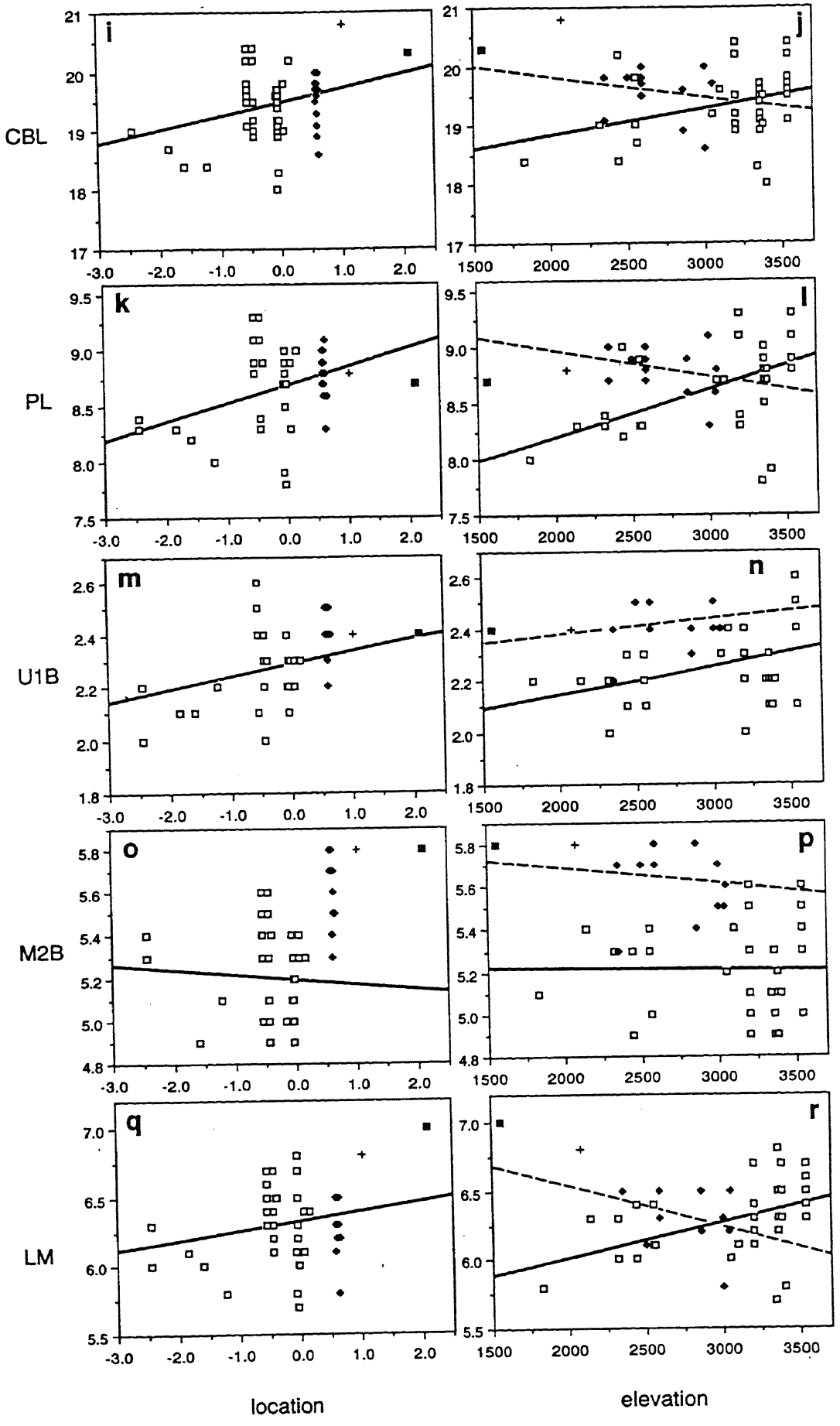


Figure 12. Plot of specimens of the C. gracilis complex on DFA canonical axis. Abbreviations are: G - Talamanca; I - Irazú; B - Volcán Barva; M - Monteverde.

Figure 13. Regressions of PCA factor scores and individual variables on location and elevation. Variable abbreviations are explained in the text. Solid regression lines in both columns represent regressions generated using specimens from Talamanca, and dashed regression lines (right column) represent regressions generated using specimens from Irazú.


a
b
c
d
e
f
g
h
factor 1
factor 2
HB
TL
location
elevation
Talamanca
V. Irazu
V. Barva
Monteverde


CBL
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elevation

or those on Irazú ($p = 0.756$, $R = 1.0\%$), indicating that there is no apparent variation in overall size with elevation in either area.

Factor 2 from the PCA of morphological variation is a shape axis representing a contrasting combination of four variables (TL & AC3 vs. HB & M2B). Regression of factor 2 on location is significant (Fig. 13c; $p = 0.028$, $R = 15.1\%$), indicating a trend of changing shape within the Talamancas. However, the difference in shape between specimens in the Talamancas and those on Irazú and Volcán Barva can not be explained by this trend. Regression of factor 2 on elevation indicates no variation of this shape axis with elevation for specimens from Talamanca (Fig. 13d; $p = 0.645$, $R = 0.7\%$) or Irazú ($p = 0.995$, $R = 0.0\%$).

Regression of head and body length (HB) on location is significant (Fig. 13e; $p = 0.015$, $R = 17.5\%$) and indicates a decrease in size from the southeast to the northwest within the Talamancas. However, this trend clearly can not explain the larger body sizes in specimens from Irazú, Volcán Barva, or Monteverde, which occur to the north. Regression of this variable on elevation indicates no elevational trends within Talamanca (Fig. 13f; $p = 0.331$, $R = 3.1\%$). However, Cryptotis from Irazú show a very significant decrease in

size with increasing elevation ($p = 0.004$, $R = 57.3\%$).

Regression of tail length (TL) on location is not significant (Fig. 13g; $p = 0.960$; $R = 0.0\%$), indicating no pattern of change within the specimens from the Talamancas. It clearly can not explain the shorter tails of the shrews from Irazú or the very long tail of the Monteverde specimen. The regressions on elevation for Talamanca (Fig. 13h; $p = 0.560$, $R = 1.1\%$) and Irazú ($p = 0.339$, $R = 8.3\%$) show no trends in tail length with elevation.

Regression of CBL on location shows no obvious pattern of clinal change (Fig. 13i; $p = 0.166$; $R = 5.7\%$). The regression of this variable on elevation for Talamancan shrews is not statistically significant, but it is close (Fig. 13j; $p = 0.065$, $R = 10.0\%$), suggesting an increase in skull length with elevation. However, this trend would not easily explain the very long skulls of the specimens from Volcán Barva and Monteverde, which are from relatively low elevations. Regression of CBL on elevation for Cryptotis from Irazú is not significant ($p = 0.503$, $R = 4.6\%$).

Regression of PL on location is close to being statistically significant (Fig. 13k; $p = 0.062$, $R = 9.3\%$), suggesting that there is a trend of increasing length of palate to the northwest in Talamanca.

Specimens from the other three areas conform to this trend. There is also a very significant trend of increasing length with elevation in Talamancan shrews (Fig. 13l; $p = 0.004$, $R = 20.9\%$). Such an elevational trend is not obvious in material from Irazú ($p = 0.269$, $R = 10.9\%$).

The variable U1B is a measure of the anterior width of the palate. Regression of U1B on location is not significant (Fig. 13m; $p = 0.136$, $R = 6.1\%$). However, regression of U1B on elevation for Talamancan shrews indicates a trend of increasing width with elevation (Fig. 13n; $p = 0.028$, $R = 13.0\%$). Regression of this variable on elevation for the shrews from Irazú shows no such trend ($p = 0.625$, $R = 2.2\%$). In fact, at any given elevation, shrews from Irazú, Volcán Barva, and Monteverde tend to have wider anterior palates than those from Talamanca, although the difference diminishes with increasing elevation.

The posterior width of the palate is assessed by M2B. Regression of M2B on location is not statistically significant (Fig. 13o; $p = 0.594$, $R = 0.8\%$), nor is regression on elevation for shrews from either Talamanca (Fig. 13p; $p = 0.908$, $R = 0.0\%$) or Irazú ($p = 0.702$, $R = 1.4\%$). As for U1B, shrews from Irazú, Volcán Barva, and Monteverde tend to have wider posterior palates than

those from Talamanca at any given elevation, but there is no convergence at higher elevations.

Regression of LM on location indicates no geographic clinal trend in this variable in Talmancan shrews (Fig. 13q; $p = 0.242$, $R = 3.8\%$). Regression on elevation, however, shows a very significant trend of increasing mandible length with elevation (Fig. 13r; $p = 0.005$, $R = 20.3\%$). Shrews from Irazú show no corresponding elevational trend ($p = 0.204$, $R = 14.2\%$), although they are generally within the size limits of Talamancan shrews at any given elevation. In contrast, specimens from Volcán Barva and Monteverde have much longer LM, which can not be accounted for by the regression on Talamanca specimens.

Because there are few specimens available from the southern part of Talamanca, and because specimens in the northern portion of the range show wide dispersion, specimens from southern Talamanca sometimes exert strong influences on regressions on location. Also, variation among specimens at single locations is sometimes quite large. Some trends or lack of trends of geographic variation in Talamancan Cryptotis may change once larger samples of these shrews from other parts of the range are available for study.

Discussion

Cryptotis within the Chiriquí and Talamancan highlands exhibit little obvious sexual dimorphism in size or shape. Of all variables tested, only ZP showed clear mean differences between sexes. The biological significance of this, if any, is unknown. No external measurements or any of the larger, commonly used cranial variables exhibited this dimorphism. Lack of even a moderately large series of sexed specimens from a single locality prevents rigorous testing for secondary sexual variation. Two-way ANOVAs permitted partitioning out of sexual and geographic components of variation in a series of specimens from three localities, but sample size remained low. DFA of sexual variation used all sexed specimens currently known from museum collections, but within-group variation was inflated by geographic variation.

Members of the *C. gracilis* group from Monteverde, Volcán Barva, Irazú, and Talamanca are morphologically distinct and are geographically isolated from each other. Trends in morphological variation within Talamancan *Cryptotis* are evident for some variables. Specimens from Talamanca show significant patterns of geographic variation in factor 2 scores and HB, and there is a possible trend in PL. An elevational cline

is suggested in CBL, and there are significant or very significant elevational changes in U1B, PL, and LM. In addition, shrews from Irazú show a very significant elevational cline for HB. However, the geographical and elevational variation seen within the Talamancan Highlands does not explain the variation seen among shrews from the four geographic areas inhabited by members of the C. gracilis group. It appears instead that they are evolving separately and represent distinct species. Two of these forms previously were described as C. gracilis and C. jacksoni, respectively. Two additional taxa represent species new to science, and their descriptions are presented below.

The time of separation of the four groups from common ancestors is unknown, but likely relates to environmental changes occurring during the end of the Wisconsinan glacial epoch and the early Holocene. Evidence from analyses of fossil pollen associations from Costa Rica indicates that Pleistocene vegetational zonation was quite different from modern vegetational patterns, and paramo reached as much as 650 m lower than its present limit during the late Wisconsinan (Martin, 1964). Studies of fossil pollen from elsewhere in the Neotropics indicate that tropical vegetation during the Wisconsinan consisted of unique communities of plants

(Bush et al., 1990). Ancestors of modern members of the C. gracilis group may have ranged freely down to elevations as low as 1000-1200 m during this time and been represented by a single, cohesive species. With the upward migration of tropical rain forest and the establishment of modern vegetational associations in Costa Rica about 10,000 years ago (Martin, 1964), the ancestors of the modern C. gracilis group were restricted to higher elevation cloud forest and paramo, and populations became geographically and genetically isolated. Further investigation of the history of these shrews awaits a definitive phylogenetic analysis of the genus.

Comparisons with other Costa Rican Shrews

Besides members of the C. gracilis group, two other species of small-eared shrews, C. parva orophila and C. nigrescens nigrescens are known to inhabit Costa Rica. Cryptotis endersi, currently known from only two specimens from the Chiriquí Cordillera of western Panama, may also occur in the Talamancan Highlands of extreme southeastern Costa Rica. Members of the C. gracilis group in Costa Rica have a number of characteristics in common which distinguish them from these three species. Characteristics which best distinguish individual members of the C. gracilis group

from these species are noted in the accounts for each taxon. Selected measurements of Costa Rican species of Cryptotis (and the two specimens of C. endersi from Panama) are presented in Tables 2 and 3.

Cryptotis parva orophila: members of the C. gracilis group differ in their larger size; longer tail relative to body length; pelage color darker, about dark brown or black both dorsally and ventrally in contrast to C. p. orophila, which is light to medium brown dorsally and has a much lighter venter; rostrum much longer, appearing arched; interorbital area much broader; usually two dorsal foramina instead of one large foramen; absolutely longer zygomatic plate, located slightly more posteriorly relative to toothrow; braincase higher and wider; upper toothrow not crowded, U4 normally in line with other unicuspids and visible in lateral view; P4, M1, M2 not deeply recessed posteriorly; M3 larger, with well developed protocone; mandible relatively longer; coronoid process joins horizontal ramus at a wide angle, creating a long distance between articular condyle and m3.

Cryptotis nigrescens nigrescens: members of the C. gracilis group differ in their generally longer tail relative to head and body length; rostrum longer,

Table 2. Selected measurements of Costa Rican taxa of Cryptotis. Abbreviations of measurements are explained in Methods section of text. The statistics presented are mean ± standard deviation of the mean, observed extremes, and number of individuals in parentheses.

HB	TL	TL/HB (%)	CBL	CB
C. endersi (2)				
73, 89	36, 49	49, 55	20.4, 21.3	9.8, 10.5
C. nigrescens nigrescens				
65 ± 5	27 ± 3	43 ± 6	18.1 ± 0.5	9.0 ± 0.2
55 - 79	20 - 34	29 - 53	17.1 - 19.2	8.6 - 9.5
(34)	(34)	(34)	(30)	(30)
C. parva orophila				
63 ± 8	21 ± 2	34 ± 4	17.1 ± 0.3	8.2 ± 0.3
48 - 77	17 - 24	29 - 42	16.7 - 17.7	7.8 - 8.8
(17)	(17)	(17)	(9)	(9)
C. gracilis				
67 ± 7	36 ± 3	55 ± 7	19.4 ± 0.6	9.7 ± 0.4
57 - 77	29 - 42	45 - 68	18.0 - 20.4	9.0 - 10.3
(33)	(33)	(33)	(35)	(34)
C. jacksoni (13)				
73 ± 5	33 ± 2	45 ± 3	19.5 ± 0.4	9.8 ± 0.3
65 - 82	29 - 36	38 - 49	18.6 - 20.0	9.4 - 10.4
Cryptotis "A" (1)				
79	39	49	20.8	9.9
Cryptotis "B" (1)				
80	46	58	20.3	-

Table 3. Relative breadth of the zygomatic plate (ZP) in Costa Rican Cryptotis, expressed as percent of palatal length (PL). The statistics presented are mean ± standard deviation of the mean, and observed extremes; number of individuals is in parentheses.

	ZP	PL	ZP/PL (%)
C. endersi (2)			
	1.9, 2.0	8.6, 9.3	20.4, 23.3
C. nigrescens nigrescens (30)			
	1.9 ± 0.2	7.7 ± 0.2	25.0 ± 1.9
	1.6 - 2.2	7.3 - 8.3	21.1 - 28.2
C. parva orophila (15)			
	1.5 ± 0.1	7.4 ± 0.2	20.7 ± 1.3
	1.4 - 1.7	7.1 - 7.8	18.9 - 23.0
C. gracilis (35)			
	1.7 ± 0.1	8.7 ± 0.4	20.2 ± 1.7
	1.5 - 2.0	7.8 - 9.3	16.5 - 22.9
C. jacksoni (13)			
	1.8 ± 0.1	8.8 ± 0.2	20.5 ± 1.1
	1.6 - 1.9	8.3 - 9.1	18.4 - 22.8
Cryptotis "A" (1)			
	2.0	8.8	22.7
Cryptotis "B" (1)			
	1.8	8.7	20.7

appearing more arched; relatively much shorter zygomatic plate; unicuspid toothrow not crowded, U4 normally in line with other unicuspids and clearly visible in lateral view; M3 larger, with well developed protocone; mandible relatively longer; coronoid process joining horizontal ramus at a wide angle, creating a long distance between articular condyle and m3.

Cryptotis endersi: members of the C. gracilis group differ in being smaller; anterior portion of the rostrum not quite as high, appearing somewhat more arched; protocone of M3 more developed; dentition not bulbous; lower articular surface of articular condyle much narrower.

Species Accounts

Cryptotis gracilis G. S. Miller, 1911

Fig. 14

Cryptotis gracilis G. S. Miller, 31 October 1911, Proc. Biol. Soc. Washington 24:221; G. G. Goodwin, 31 December 1946, Bull. Amer. Mus. Nat. Hist. 87:289; E. R. Hall and K. R. Kelson, 31 March 1959, The Mammals of North America 1:61; J. R. Choate, 30 December 1970, Univ. Kansas Pub., Mus. Nat. Hist. 19:281 (in part); E. R. Hall, 3 April 1981, The Mammals of North America 1:63 (in part).

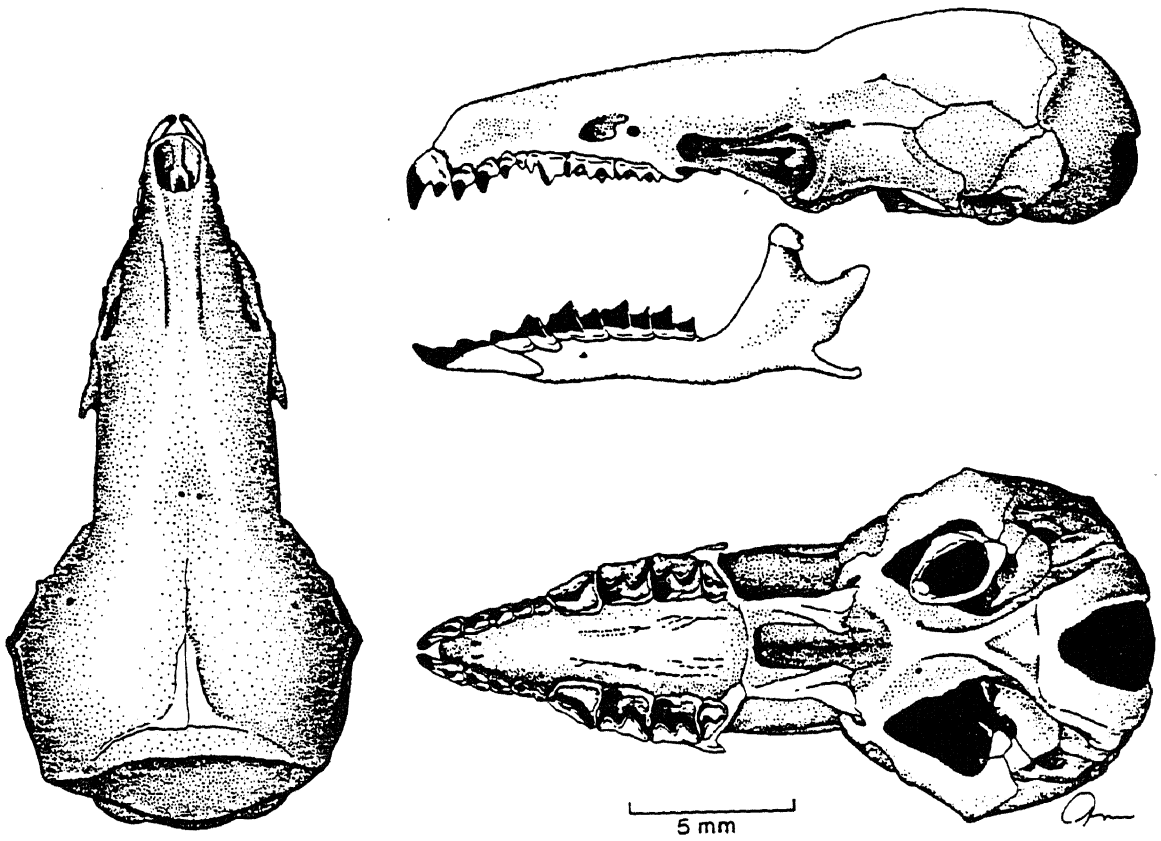

Figure 14. Dorsal and ventral views of the skull and lateral view of the skull and mandible of C. gracilis (LSU 12659).

Cryptotis orophila W. P. Harris, 8 October 1943, Occas. Papers Mus. Zool., Univ. Michigan 476:7. [The name orophila now is applied to a subspecies of C. parva. Harris (1943) incorrectly identified this specimen.]

Holotype.--Skin and skull of subadult, sex unknown, U.S. National Museum number 12236/38471; obtained by William M. Gabb (collector number 19) on an unknown date.

Type locality.--Costa Rica, Limón Province, head of Río Lari, near base of Pico Blanco [= Cerro Kámuk]; ca. 6000 ft [ca. 1830 m].

Distribution.--Above ca. 1800 m in the Talamancan Highlands of Costa Rica and the adjacent Chiriquí Highlands of western Panama.

Description.--Medium size Cryptotis (Table 2); tail long, averaging 36 mm, or about 55% of head and body length; dorsal pelage Fuscous/ Chaetura Drab/Fuscous-Black/Chaetura Black, between Hair Brown and Chaetura Drab on occasion; lateral pelage Hair Brown/Fuscous/ Chaetura Drab/Chaetura Black, occasionally Drab; venter slightly lighter than dorsum, Drab/Hair Brown/Fuscous, occasionally Drab; dorsal hairs typically 6 to 8 mm in length.

Rostrum very long, narrow; anterior portion of rostrum long, low, and narrow, appearing strongly arched downward in lateral view; interorbital area wide; usually two dorsal foramina (74%, n = 34), both usually of medium size and close together along midline of the skull; braincase high and wide; zygomatic plate relatively short (Table 3); anterior border of zygomatic plate from metastyle of M1 to parastyle of M2, posterior border from parastyle to middle of M3 and well anterior to maxillary process; upper toothrow uncrowded; U4 usually in line with other unicuspids and clearly visible in lateral view of skull; posterior borders of P4, M1, M2 only slightly recessed; M3 with paracrista, precentrocrista, reduced postcentrocrista, and well developed metacone and protocone. Dentition not bulbous.

Mandible long, thin; coronoid process narrow, joining horizontal ramus at a very wide angle; distance between articular condyle and m3 long; viewed posteriorly, articular process much taller than broad; lower sigmoid notch of moderate depth; posterior border of lower incisor extends about to the posterior cusp of p4; talonid of m3 with hypoconid and entoconid.

Comparisons.--Comparisons with other species of the C.

Table 4. Selected measurements of members of the C. gracilis group. Abbreviations of measurements are explained in Methods section of text. The statistics presented are mean ± standard deviation of the mean, and observed extremes. Number of individuals is in parentheses.

	C. gracilis (38)	C. jacksoni (14)	Cryptotis "A" (1)	Cryptotis "B" (1)
PO	4.6 ± 0.2 4.0 - 4.9 (37)	4.7 ± 0.2 4.3 - 5.2	4.7	5.1
U1B	2.3 ± 0.1 2.0 - 2.6	2.4 ± 0.1 2.2 - 2.5	2.4	2.4
M2B	5.2 ± 0.2 4.9 - 5.6	5.6 ± 0.2 5.3 - 5.8	5.8	5.8
TRL	7.5 ± 0.3 6.9 - 8.0	7.6 ± 0.3 7.0 - 8.1	7.9	8.1
UTR	2.5 ± 0.2 2.3 - 2.9	2.6 ± 0.1 2.4 - 2.7	2.6	2.8
M1W	1.6 ± 0.1 1.4 - 1.8	1.7 ± 0.1 1.6 - 1.8	1.8	1.8
LM	6.3 ± 0.3 5.7 - 6.8	6.3 ± 0.2 5.8 - 6.5	6.8	7.0
HCP	4.0 ± 0.2 3.3 - 4.4	4.1 ± 0.1 3.9 - 4.3	4.4	4.5
HAC	3.7 ± 0.2 3.3 - 4.0	3.7 ± 0.2 3.3 - 3.9	3.1	4.1
BAP	2.9 ± 0.1 2.7 - 3.2	3.0 ± 0.1 2.7 - 3.1	3.0	3.2
AC3	5.0 ± 0.2 4.4 - 5.5	5.0 ± 0.2 4.7 - 5.3	5.3	5.3
TRD	5.9 ± 0.2 5.5 - 6.4	6.1 ± 0.2 5.7 - 6.3	6.3	6.4
Lm1	1.6 ± 0.1 1.5 - 1.8	1.7 ± 0.1 1.6 - 1.8	1.8	1.8

gracilis species group are given with accounts for those species. Selected measurements are presented in Tables 2-4.

Cryptotis endersi: C. gracilis differs in having a relatively narrower rostrum, palate, and upper molariform dentition; anterior portion of rostrum lower, appearing more downwardly arched; M3 with more distinct protocone and metacone.

Cryptotis nigrescens nigrescens: C. gracilis differs in having a longer, narrower, more arched rostrum; M3 with well developed protocone, postcentrocrista, and metacone; relatively longer mandible; articular process tall and relatively narrow; deeper lower sigmoid notch; talonid of m3 with hypoconid and entoconid.

Cryptotis parva orophila: C. gracilis differs in having a longer, narrower, and more arched rostrum; M3 with well developed protocone, mesostyle, and metacone; longer mandible; articular process taller than broad; deep lower sigmoid notch; talonid of m3 with hypoconid and entoconid.

Remarks.--Pelage coloration normally is quite consistent in this species. The most deviant coloration is on a specimen from Cerro de la Muerte (UMMZ 115403), which is

a bit lighter, between Hair Brown and Chaetura Drab dorsally, and Drab laterally and ventrally. A specimen from the nearby Cerro Buena Vista (MSB 28339) is intermediate in color, Fuscous dorsally, close to Fuscous on the sides, close to Hair Brown ventrally. This suggests local variation in pelage may be present on Cerro de la Muerte, perhaps coinciding with the open vegetation there. However, lack of lighter coloration on specimens from Cerro Chirripó, where similar ecological conditions dominate, suggests that the lighter coloration may be individual variation or due to some other reason [postmortem bleaching?]. We consider C. gracilis a monotypic species.

One Cryptotis gracilis (UMMZ 62885), collected at Las Vueltas by Austin Smith in 1931, has the elevation 8000 ft clearly written on the original skin tag. However, Harris (1943) reported that this and a number of other specimens collected "near timberline" on Cerro Vueltas came from an elevation of ca. 11,000-11,300 ft. Goodwin (1946) reported that the specimen was collected at 8000 ft. Choate (1970) reiterated that the specimen was from ca. 11,000 ft. However, the highest point on Cerro Vueltas is 3156 m (= ca. 10,355 ft).

Cerro de la Muerte [= Cerro Buenavista] occurs just inside San José Province, along the border between San

José and Cartago Provinces. Original skin tags of two specimens (UMMZ 112000, 115403) from near this peak state that they came from Cartago Province, and thus may have come from the northern slope, north of the provincial line. Similarly, a specimen from nearby Hotel Georgina (USNM 556131), which is located in Cartago Province, may have come from just south of the line in San José based on the information on its skin tag. The maps of Costa Rica available to collectors in the 1960s and 1970s do not reflect the level of accuracy that we can achieve today.

Reproductive data for C. gracilis previously were summarized by Choate (1970). No data exist for the period from September through December, for which no specimens, male or female, are known in collections. An adult female (USNM 322994) with a single embryo was taken on 8 March on Cerro Punta. Another adult female (LSU 12650), caught on 6 April on Cerro Asunción, had a swollen right uterine horn, suggesting a recent pregnancy. A second (LSU 12658 - not 12657, as reported by Choate, 1970), with four embryos, was captured on Cerro Chirripó on 21 July. Females without embryos are recorded from the months of January (n = 6), April (1), and July (1). Males with enlarged testes have been captured in January, March, April, and July. Our

inspection of study skins and fluid-preserved specimens of C. gracilis shows that lateral glands are well developed on males in January (1), March (2), April (1), and July (5). On dried study skins, these glands appear as paired, oval patches of often darker, thicker skin approximately 8 x 5 mm and lacking long guard hairs or normal underfur, but sometimes hidden by surrounding guard hairs. Upon initial inspection, these appear as areas where the skin has "slipped" due to beginning stages of decomposition. However, closer inspection with a binocular microscope reveals a light covering of short, whitish hairs, arranged in a symmetrical pattern. Lateral glands are known to exist in all genera of modern soricids, where they are often easily observed in males, but are much smaller and more difficult to identify in females (Murariu, 1976; Bee et al., 1980). In male Blarina, these glands show increased activity with growth of the testes (Eadie, 1938), and female C. parva have been observed to sometimes sniff the lateral glands of a male when approached by him (Kivett and Mock, 1980). Very likely, the glands serve a function in sexual and social communication, but it has been suggested also that the strong odor associated with soricid dermal glands serves primarily as a deterrant to potential predators (Murariu, 1976). Among Cryptotis,

lateral glands previously were reported from only C. parva.

Cryptotis gracilis is a high elevation species. Most specimens having been captured between elevations of ca. 2315 to 3535 m in Costa Rica and Panama. Only the holotype, reportly collected at ca. 6000 ft [ca. 1830 m], is from lower that 2300 m. Most specimens were taken in cloud forest or paramo.

Cryptotis jacksoni G. G. Goodwin, 1944

Fig. 15

Cryptotis jacksoni G. G. Goodwin, 10 December 1944, Amer. Mus. Novit. 1267:1; G. G. Goodwin, 31 December 1946, Bull. Amer. Mus. Nat. Hist. 87:289; E. R. Hall and K. R. Kelson, 31 March 1959, The Mammals of North America 1:61.

C.[ryptotis] orophila G. S. Miller, 1911, Proc. Biol. Soc. Wash. 24:221 (see Goodwin, 1944).

Cryptotis gracilis J. R. Choate, 30 December 1970, Univ. Kansas Publs., Mus. Nat. Hist. 19:281 (in part); E. R. Hall, 3 April 1981, The Mammals of North America 1:63 (in part).

Holotype.--Skin and skull of adult, U.S. National Museum

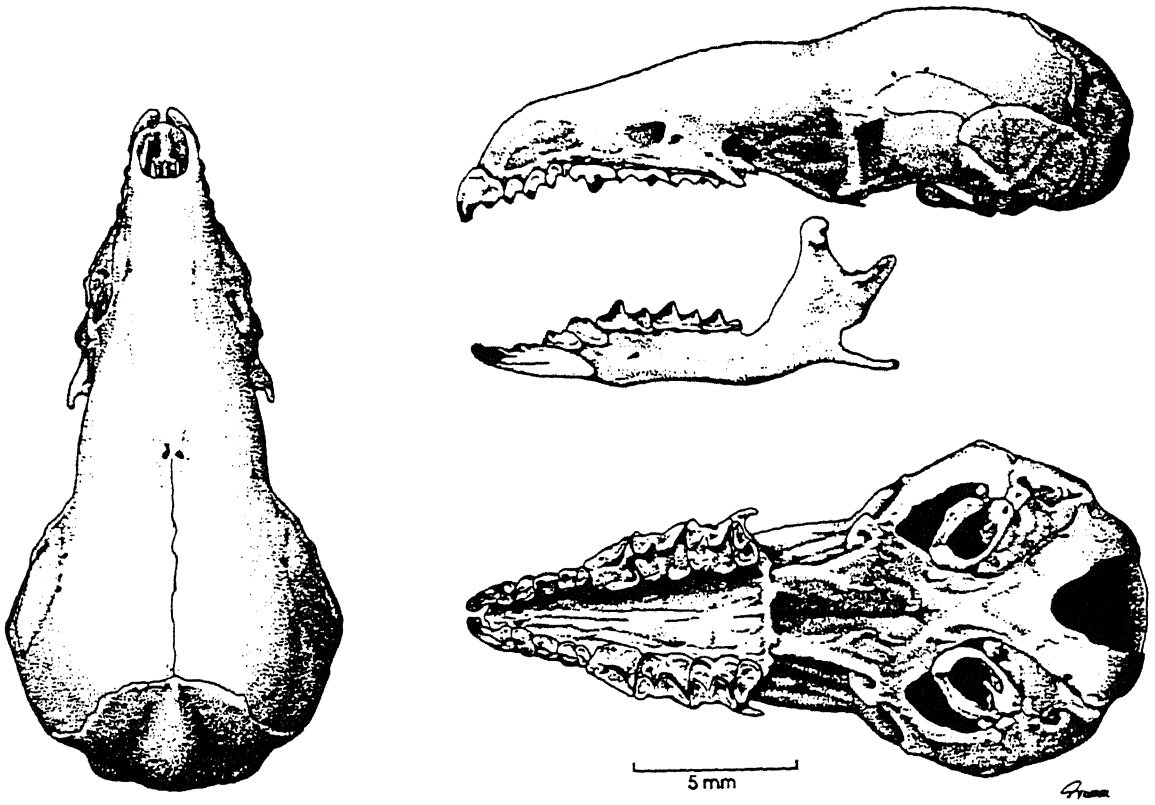

Figure 15. Dorsal and ventral views of the skull and lateral view of the skull and mandible of C. jacksoni (UMMZ 122448).

number 116649 collected by M. Cary (collector number 540/3549) on 27 February 1902. The original skin tag associated with this specimen indicates that Cary identified this specimen as a female, and Goodwin (1944) reported it as such when he described C. jacksoni. However, there is a pair of well-developed lateral glands (measuring approximately 6 x 4 mm) on the holotype, which almost certainly indicate that it was a male.

Type locality.--Costa Rica, Cartago Province, Volcán Irazú.

Distribution.--Above 2300 m on Volcán Irazú and adjoining Volcán Turrialba.

Description.--Medium size Cryptotis (Table 2); tail long, averaging 33 mm, or ca. 45% of head and body length; dorsal pelage Fuscous/ Chaetura Drab/Chaetura Black; lateral pelage Hair Brown/Fuscous/ Chaetura Drab; venter slightly lighter than dorsum, Light Drab/ Drab/Hair Brown/Fuscous; dorsal hairs typically 5 to 7 mm in length.

Rostrum very long, narrow; anterior portion of rostrum long and low, appearing strongly arched downward in lateral view; interorbital area wide, appearing inflated; usually two dorsal foramina (93%, n = 15),

both usually of medium size and close together along midline of the skull; braincase high and wide; zygomatic plate relatively short; anterior border of zygomatic plate from metastyle of M1 to parastyle of M2, posterior border from parastyle to middle of M3 and well anterior to maxillary process; upper toothrow uncrowded; U4 usually in line with other unicuspids and clearly visible in lateral view of skull; posterior borders of P4, M1, M2 only slightly recessed; M3 with paracrista, precentrocrista, reduced postcentrocrista, and well developed metacone and protocone. Dentition not bulbous.

Mandible long, thin; coronoid process narrow and joining horizontal ramus at a very wide angle; distance between articular condyle and m3 long; viewed posteriorly, articular process much taller than broad; lower sigmoid notch of moderate depth; posterior border of lower incisor extends about to posterior cusp of p4; talonid of m3 with hypoconid and entoconid.

Comparisons.--Selected measurements are presented in Tables 2-4.

Cryptotis gracilis: C. jacksoni averages slightly lighter in dorsal pelage coloration; it is generally larger in most dimensions, but has a relatively shorter

tail (Fig. 16); much wider rostrum, palate, and upper molars (Fig. 17).

Cryptotis endersi: M3 of C. jacksoni has a more distinct protocone and metacone.

Cryptotis nigrescens nigrescens: C. jacksoni differs in having a longer, narrower, more arched rostrum; M3 with well developed protocone and metacone; relatively longer mandible; articular process tall and relatively narrow; deeper lower sigmoid notch; talonid of m3 with hypoconid and entoconid.

Cryptotis parva orophila: C. jacksoni differs in having a much longer, narrower, and more arched rostrum; M3 with well developed protocone, mesostyle, and metacone; longer mandible; articular process taller than broad; deeper lower sigmoid notch; talonid of m3 with hypoconid and entoconid.

Remarks.--Cryptotis jacksoni is a high elevation species that has been taken between ca. 2350-3180 m on Volcán Irazú and Volcán Turrialba. Volcán Irazú is an active volcano, and vegetation does not occur at its highest elevations (up to 3432 m) because of recent volcanic activity. The range of Cryptotis jacksoni probably extends as far up as there is vegetation, as well as to

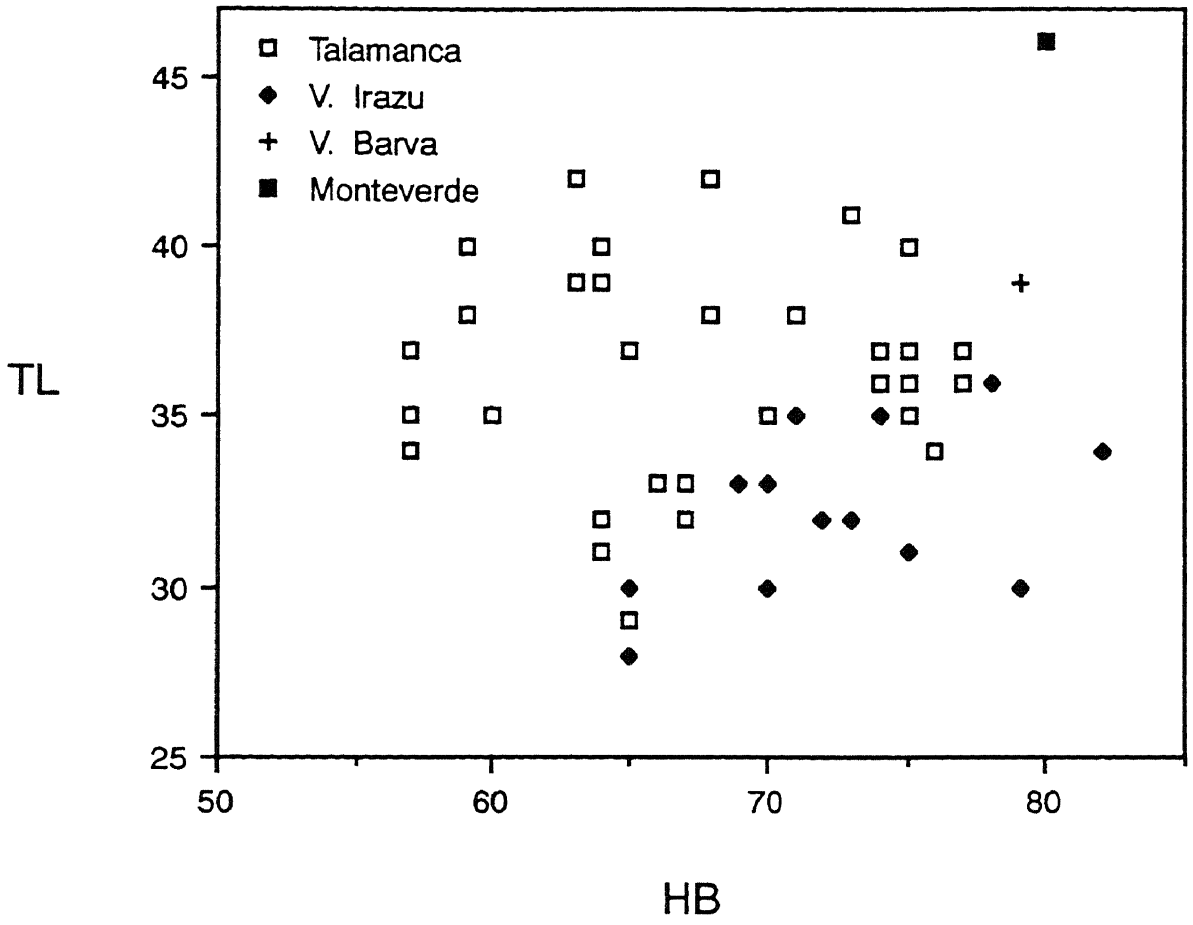

Figure 16. Plot of head and body length (HB) against tail length (TL) for specimens of the C. gracilis group.

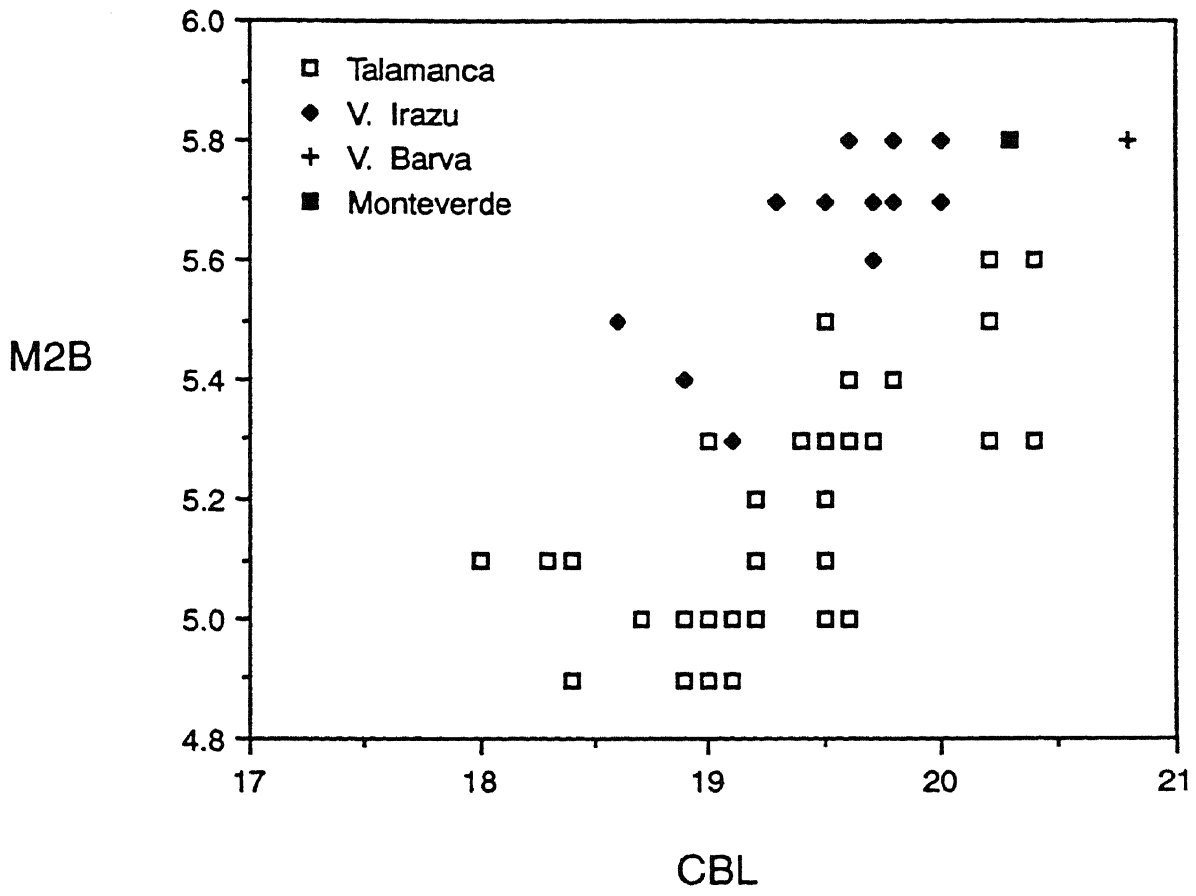

Figure 17. Plot of condylobasal length (CBL) against width across the M2s (M2B) for specimens of the C. gracilis group.

the highest portions of dormant Volcán Turrialba (up to 3328 m).

Both C. gracilis and C. jacksoni are high elevation shrews which occur above ca. 1800 m. There is a physiographic gap between the range of C. gracilis in the Talamancan Highlands and that of C. jacksoni to the north on Volcán Irazú and Volcán Turrialba. The highest connection between these two highland areas is by the Cerros de La Carpintera, which extend well below 1600 m at their lowest point and never reach 2000 m. It thus appears extremely unlikely that C. gracilis and C. jacksoni have been in contact with each other in the recent past.

Cryptotis jacksoni has a wider skull than Talamancan C. gracilis, especially in the rostrum, palate, and the postorbital area, in addition to wider upper premolars and molars, and a relatively shorter tail. Goodwin (1944) noted the cranial differences between these two taxa when he first described C. jacksoni. Miller (1911) also noted some of the cranial differences when he described C. gracilis. In his description, Miller "used the type of C. jacksoni for comparison, assuming it to be a topotype of C. orophila" (Goodwin, 1944:2). Choate (1970) felt that the shrews from the Volcán Irazú region fell within the range of variation of C.

gracilis, and he synonomized C. jacksoni with C. gracilis. Now that more specimens from Volcán Irazú and Volcán Turrialba are available, it is clear that the cranial differences are consistent. We consider C. jacksoni a monotypic species.

There are few reproductive data available for C. jacksoni. A parous, adult female (KU 135356) was not carrying any embryos on 1 November, and an adult male (UMMZ 122448) had well developed lateral glands on 14 August. No specimens of this species are known from January, March, May through July, September, October, or December.

Cryptotis "A"

Fig. 18

Cryptotis gracilis J. R. Choate, 30 December 1970, Univ. Kansas Publs. Mus. Nat. Hist. 19:281 (in part); E. R. Hall, 3 April 1981, The Mammals of North America 1:63 (in part).

Cryptotis sp. R. M. Timm et al., December 1989, North American Fauna 75:22.

Holotype.--Skin and skull of adult male, University of Michigan Museum of Zoology number 116377; collected by E. T. Hooper (collector number 5648) 28 July 1968; skull

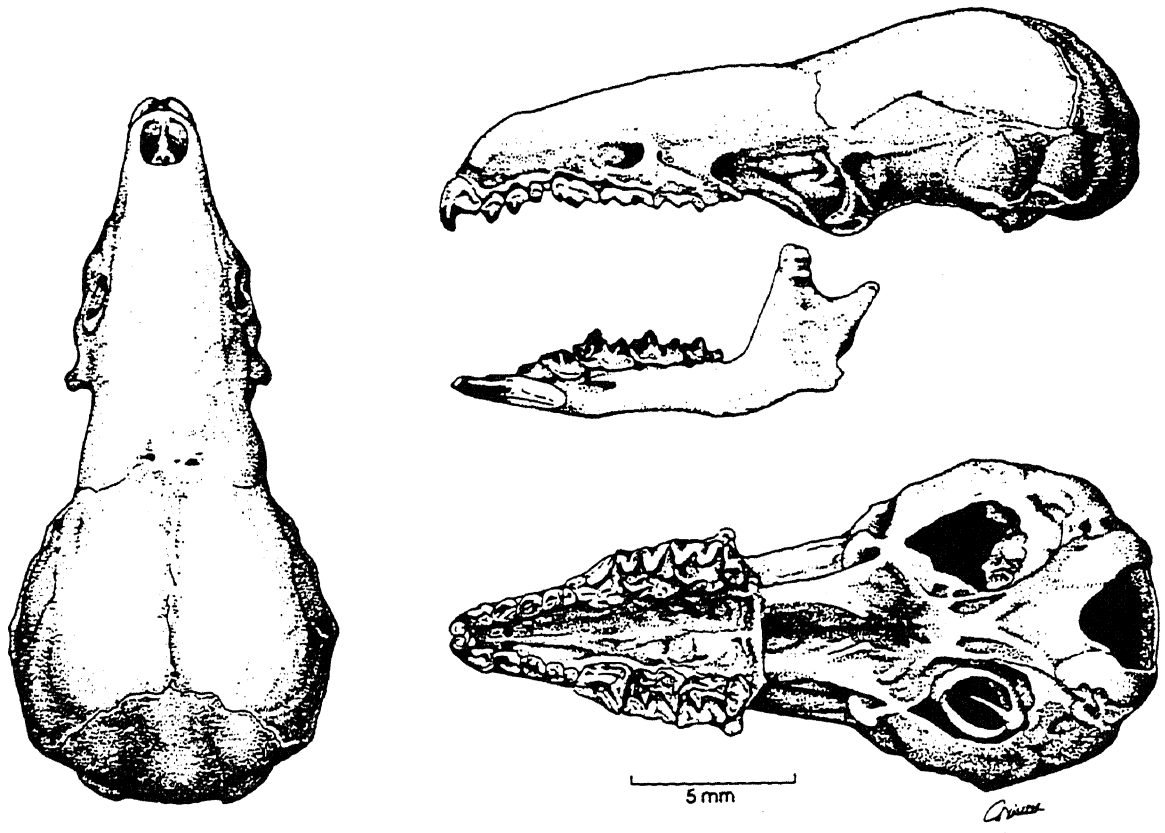

Figure 18. Dorsal and ventral views of the skull and lateral view of the skull and mandible of Cryptotis "A" (UMMZ 116377).

is in excellent condition, the skin is missing a small patch of fur posterior to the left lateral gland.

Type locality.--Costa Rica, Heredia Province, 11 km NNE of Heredia along Route 113; specimen was taken in a stump in pasture above Alto de Roble [a saddle between the Pacific and Caribbean drainages located between Cerro Chompipe and Volcán Barva proper, ca. 10°05'30"N, 84°04'30"E]; 2080 m.

Distribution.--Known only from type locality. This species probably inhabits cloud forests mostly above 2000 m on Volcán Barva. It may occur also on Volcán Poas and as far west as the highlands east and northeast of Zarcero.

Diagnosis.--A medium size species of the genus Cryptotis, characterized by its long and thick pelage, similar, dark dorsal and ventral coloration, long tail, long snout, widely spaced dorsal foramina, unrecessed upper molariform dentition, complex M3, long mandible, wide angle between the articular condyle and the horizontal ramus, tall and narrow articular process, and simple talonid.

Description of holotype.--Medium size Cryptotis (Table 2); tail long, 39 mm, or 49% of head and body length;

pelage long, thick, dorsal hairs about 6 to 7 mm long; dorsal pelage between Chaetura Black and Fuscous, nearer to Fuscous; lateral pelage between Chaetura Drab and Hair Brown; ventrum Hair Brown.

Rostrum long, of moderate breadth; anterior portion of rostrum long, high, appearing somewhat arched downward; interorbital area wide; two widely spaced dorsal foramina: left foramen of medium size, right foramen very large; braincase high, wide; zygomatic plate relatively narrow; anterior border of zygomatic plate just anterior to metastyle of M1, posterior border just posterior parastyle of M3, near middle of maxillary process; upper toothrow not particularly crowded; U4 in line with other unicuspids, visible in lateral view; posterior borders of P4, M1, M2 only very slightly recessed; M3 with well-developed paracrista and precentrocrista, and distinct protocone; pigmentation on the posterior cingulum of M3 suggests the presence of a vestigial mesostyle or cusplet; dentition not bulbous.

Mandible long, of moderate breadth; coronoid process of moderate breadth; coronoid process joins horizontal ramus at a wide angle; viewed posteriorly, articular condyle much taller than broad; distance between articular condyle and m3 long; lower sigmoid notch of moderate depth; posterior border of lower incisor extends

about to middle of p4; talonid of m3 with only hypoconid.

Comparisons.--Selected measurements are presented in Tables 2-4.

Cryptotis gracilis: Cryptotis "A" is larger in head and body length and in condylobasal length, and has a relatively shorter tail; much wider rostrum, palate, and upper molariform dentition; dorsal foramina widely spaced; length of zygomatic plate averages longer; M3 relatively smaller, lacking well-developed metacone; mandible somewhat broader; talonid of m3 with only hypoconid, lacking entoconid.

Cryptotis jacksoni: Cryptotis "A" is generally larger in head and body length and in condylobasal length, and it has an absolutely longer tail; widely spaced dorsal foramina; relatively and absolutely longer zygomatic plate; M3 relatively smaller, lacking a well-developed metacone; mandible somewhat broader; talonid of m3 with only hypoconid.

Cryptotis endersi: Interorbital area of Cryptotis "A" less inflated; dorsal foramina set widely apart; lower articulation of articular condyle much narrower; only hypoconid in talonid of m3.

Cryptotis nigrescens nigrescens: Cryptotis "A" is larger; rostrum long, arched; dorsal foramina widely spaced; M3 with a distinct, pigmented protocone; articular condyle relatively taller; lower sigmoid notch deeper.

Cryptotis parva orophila: Cryptotis "A" has a longer, more arched rostrum; two widely spaced dorsal foramina; M3 with distinct protocone; mandible relatively and absolutely longer and broader; articular condyle taller than broad; lower sigmoid notch deeper.

Remarks.--The holotype of Cryptotis "A" was taken at 2080 m, well below the lowest elevations known for C. jacksoni and most specimens of C. gracilis. The species likely ranges up to the highest vegetated portions of Volcán Barva (2906 m) and, possibly, the adjacent, active Volcán Poas (2704 m). The lowest extent of its range is difficult to determine. On Volcán Barva, only C. parva has been taken at 1800 m and below on the western slopes (Timm et al., 1989). The highland range of Cryptotis "A" is separated from the range of C. jacksoni on Volcán Irazú and Volcán Turrialba by a valley that extends to below 1500 m. It is unlikely that either species of shrew has crossed this valley in the recent past. Volcán Poas and Volcán Barva are

similarly separated from the Cordillera de Tilarán, the closest highland to the northwest, by lower elevational areas that extend below 1400 m.

The holotype and only known specimen, captured on 28 July, has paired lateral glands similar to those of C. gracilis. These appear as areas of darker skin, ca. 6 x 4 mm, and devoid of guard hairs or underfur. Instead, the lateral glands have a sparse covering of very short, whitish hairs. No other reproductive information is available for Cryptotis "A".

Cryptotis "B"

Fig. 19

Holotype.--Fluid-preserved adult female with skull removed; University of Kansas Museum of Natural History number 134852; collected and preserved in fluid by Walter James; presented to R. K. LaVal (collector number 3115) 13 August 1973.

Type locality: Costa Rica, Puntarenas Province, Monteverde, Monteverde Cloud Forest Preserve, in cloud forest at the continental divide (ca. 10°18'N, 84°47'W); based on current topographic maps, the elevation of the divide at the crossing is ca. 1560 m.

Distribution.--Known only from type locality, this

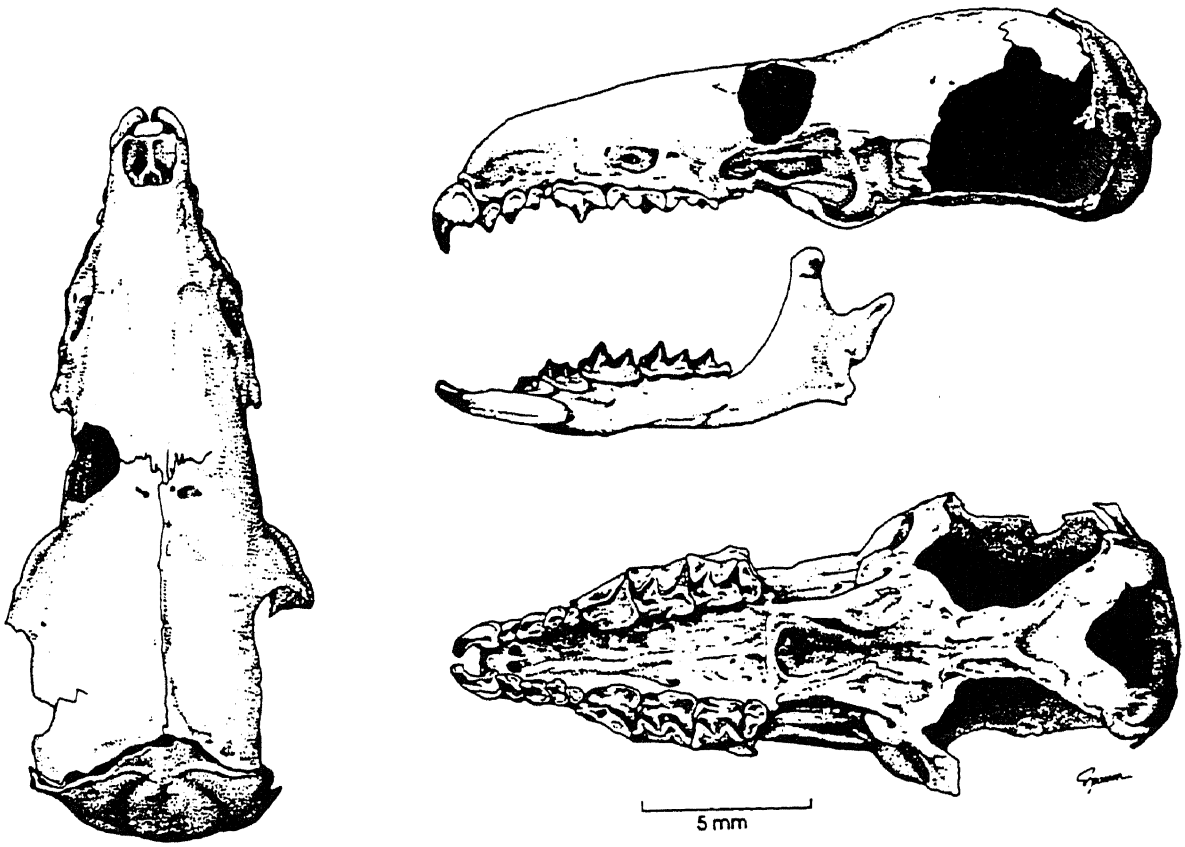

Figure 19. Dorsal and ventral views of the skull and lateral view of the skull and mandible of Cryptotis "B" n. sp. (KU 134852).

species is perhaps restricted to the highest parts of the Cordillera de Tilarán, above ca. 1500 m.

Diagnosis.--A medium size species of the genus Cryptotis, characterized by its similar, dark dorsal and ventral coloration, very long tail, long snout, widely spaced dorsal foramina, unrecessed upper molariform dentition, complex M3, very long and broad mandible, wide angle between the articular condyle and the horizontal ramus, tall and narrow articular process, and complex talonid.

Description of holotype.--Medium size Cryptotis (Table 2); tail quite long, 46 mm, or about 58% of head and body length; snout long and broad; the very dark pelage of the fluid-preserved holotype appears to be similar to C. gracilis; ventrum nearly as dark as dorsum.

Rostrum long, wide; anterior portion of rostrum long, high, appearing somewhat arched downward; interorbital area wide, appearing somewhat inflated; two dorsal foramina, widely spaced, widely rounded; right dorsal foramen large with a second, very small side branch, left foramen of medium size; braincase high; zygomatic plate relatively short; anterior border of zygomatic plate at anterior portion of metastyle of M1, posterior border at parastyle of M3 and about middle of maxillary

process; upper toothrow not crowded; U4 in line with other unicuspids (RU4 slightly displaced medially), visible in lateral view of skull; posterior borders of P4, M1, M2 only slightly recessed; M3 with paracrista, precentrocrista, reduced postcentrocrista, and well developed protocone; pigmentation on the posterior cingulum of M3 suggests the presence of a well-developed mesostyle, but M3 is too worn to be certain; dentition not bulbous.

Mandible very long, broad; coronoid process of moderate breadth; coronoid process joins horizontal ramus at a wide angle; distance between articular condyle and m3 long; viewed posteriorly, articular process much taller than broad; lower sigmoid notch of moderate depth; posterior border of lower incisor extends to about middle of p4; talonid of m3 with hypoconid and entoconid.

Comparisons.--*Cryptotis monteverdensis* has the absolutely longest tail and absolutely longest mandible of any member of the *C. gracilis* group. Selected measurements are presented in Tables 2-4.

Cryptotis gracilis: *Cryptotis* "B" differs in being absolutely larger in most dimensions; wider rostrum, palate, and upper molariform dentition; anterior portion

of rostrum higher, appearing less downwardly arched; dorsal foramina more widely separated; M3 relatively smaller; mandible relatively longer and broader.

Cryptotis jacksoni: Cryptotis "B" differs in being absolutely larger in most dimensions; anterior portion of rostrum higher, appearing less downwardly arched; dorsal foramina widely separated; M3 relatively smaller; mandible relatively longer and broader.

Cryptotis "A": Cryptotis "B" differs in having a more inflated interorbital area; M3 possessing a distinct metacone; mandible longer and broader; talonid of m3 with both hypoconid and entoconid.

Cryptotis endersi: Cryptotis "B" differs in having widely spaced dorsal foramina; mandible relatively much longer; lower articulation of articular condyle much narrower.

Cryptotis nigrescens nigrescens: Cryptotis "B" differs in its longer, more arched rostrum; M3 with well developed protocone; longer and broader mandible; articular process tall and narrow; talonid of m3 with hypoconid and entoconid.

Cryptotis parva orophila: Cryptotis "B" differs in

having two widely spaced dorsal foramina instead of one large foramen; M3 larger with distinct protocone; mandible absolutely longer and broader; articular process taller and narrower; talonid of m3 with hypoconid and entoconid.

Remarks.--The holotype of Cryptotis "B" is from an elevation of ca. 1560 m, nearly 300 m lower than any specimen of C. gracilis, more than 700 m lower than any known specimen of C. jacksoni, and nearly 500 m lower than the holotype of Cryptotis "A". The Cordillera de Tilarán, where Cryptotis "B" occurs, in no place reaches an elevation of 2000 m. This is clearly the lowest ranging member of the C. gracilis group.

Cryptotis monteverdensis may be the rarest, most geographically restricted member of the C. gracilis group. The type locality, Monteverde, is the best represented locality for Cryptotis in Central America. In 1989 we spent 20 days working in and around the Monteverde Cloud Forest Reserve trapping for shrews with pitfalls, snap traps, and Sherman live traps. We collected 13 Cryptotis and obtained 7 more from local residents who found them dead on a road or path, or in the possession of their cat. In addition, we examined 28 other specimens of Cryptotis from Monteverde in various systematic collections. Despite this collecting

effort and large sample size, there remains a single specimen, the holotype, of Cryptotis "B". All other shrews from the Monteverde area are C. nigrescens.

Key to the Shrews of Costa Rica

1. Rostrum elongate, appearing somewhat arched; upper toothrow not crowded; protocone present on M3; anterior border of coronoid process slopes gently toward horizontal ramus 2

2. Size large; protocone on M3 present, but not particularly well developed; dentition bulbous ..... C. endersi

2'. Size medium to large; protocone on M3 distinct, pigmented; dentition not bulbous 3

3. Dorsal foramina close to frontal suture; anterior of rostrum low 4

4. Tail relatively long, averaging 55% of head and body length; rostrum relatively uninflated; rostrum, palate, and upper molars very narrow.... C. gracilis

4'. Tail relatively short, averaging 44% of head and body length; rostrum inflated, quite wide; palate and upper molars of normal width..... C. jacksoni

3'. Dorsal foramina widely spaced; anterior of rostrum relatively high 5

5. Rostrum relatively uninflated; M3 lacks metacone; mandible of normal length; talonid of m3 consists only of hypoconid ..... Cryptotis "A"

5'. Rostrum inflated, quite wide; M3 with metacone; mandible quite long, relatively broad; hypoconid and entoconid in talonid of m3 ..... Cryptotis "B"

1'. Rostrum relatively short and broad, not especially arched; upper toothrow crowded; protocone absent on M3; coronoid process joins horizontal ramus at nearly a right angle 6

6. Pelage brown, or brownish gray, venter noticeably lighter than dorsum; posterior margin of P4, M1, M2 deeply recessed; tail relatively short, 17-24 mm long, or averaging 33% (range: 29-40%) of head and body length ..... C. parva orophila

6'. Pelage dark gray or blackish in appearance, venter not appreciably lighter than dorsum; posterior margin of P4, M1, M2 not deeply recessed; tail relatively long, 20-34 mm long, or averaging 42% (range: 29-53%) of head and body length

..... C. nigrescens nigrescens

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Specimens Examined

Cryptotis gracilis (42).--**COSTA RICA:** CARTAGO: Cerro Asunción, 11,000-11,100 ft (10 LSU); Cerro de la Muerte, 3335 m (1 UMMZ); N side summit, Pan American Highway (Cerro de la Muerte) (1 UMMZ); Parque Nacional Chirripó (1 USNM) LIMON: near base of Pico Blanco [= Cerro Kámuk], head of Río Lari, ca. 6000 ft. (1 USNM - holotype); Río Teribe [= Río Tararia], Valle El Silencio, Río Cotón, 8000 ft (1 USNM); SAN JOSE: Cerro Buena Vista, near Cerro de la Muerte [ca. 3300-3490 m] (1 MSB); Cerro Chirripó, Headwaters of Río Talari, 11,600 ft (8 LSU); Cerro de la Muerte, Hotel [La] Georgina, 3100 m (1 USNM); Cerro Estaquero, 10,000 ft (1 LSU); La Piedra, ca. 4 mi SW Cerro Chirripó, 10,500 ft

(6 LSU); Las Vueltas, 8000 ft (1 UMMZ); San Gerardo de Dota, ca. 2400-2700 m (2 KU); **PANAMA:** BOCAS DEL TORO: Cerro Fabrega, 8400 ft (1 USNM); 17.5 km NNW of El Volcán, NE of Cerro Pando, 8°56'30"N, 82°42'15"W, 2180 m (2 USNM); CHIRIQUI: Cerro Punta, Boquete Trail, 7600 ft (3 USNM); 17 km NNW of El Volcán, head of Río Candela, 8°54'50"N, 82°43'W, 2000 m (1 USNM).

Additional record (1).--**COSTA RICA:** SAN JOSE: Villa Mills, Cerro de la Muerte (1 UMMZ).

C. jacksoni (15).--**COSTA RICA:** CARTAGO: Volcán Irazú, Finca Coliblanco, 2350 m (2 UMMZ); Volcán Irazú, 0.25 mi N of San Juan Chicoa, 2860 m (1 UMMZ); Volcán Irazú, 2.5 km NE of San Juan Chicoa, 3050 m (1 UMMZ); Volcán Irazú, 5.7 km NE of San Juan Chicoa, 3040 m (1 UMMZ); Volcán Irazú, locality 6A, 3000 m [triangular area formed by Route 8, Río Birris, and a tributary] (1 UMMZ); Volcán Irazú, old entrance to Coliblanco, 2860 m [intersection of Route 8 and road to Coliblanco] (2 UMMZ); Volcán Irazú, Highway Route 8, 3180 m (1 UMMZ); Volcán Irazú, 2500 m (1 KU); Volcán Irazú (1 USNM - holotype); Volcán Turrialba, Hacienda El Retiro, 2590 m (4 UMMZ).

Cryptotis "A" (1).--**COSTA RICA:** HEREDIA: Alto de Roble, 11 km NNE of Heredia, 2080 m (1 UMMZ - holotype).

Cryptotis "B" (1).--**COSTA RICA:** PUNTARENAS: Monteverde, Monteverde Cloud Forest Reserve, ca. 1560 m (1 KU - holotype).

C. endersi (2).--PANAMA: BOCAS DEL TORO: Cylindro [not in Chiriquí Province, see Choate, 1970:286-287](1 ANSP - holotype); BOCAS DEL TORO-CHIRIQUI boundary: Cerro Bollo, 3.5 km E Escopeta, 1800-1856 m (1 USNM).

C. nigrescens nigrescens (54).--**COSTA RICA:** ALAJUELA: Monteverde Cloud Forest Reserve, 1580-1600 m (3 KU); Monteverde Cloud Forest Reserve, Peñas Blancas Valley, 870 m (2 KU); ALAJUELA/GUANACASTE border: Monteverde Cloud Forest Reserve, 1580 m (1 KU); GUANACASTE/PUNTARENAS border: near Monteverde, Cerro Amigos, 1750-1790 m (3 KU); PUNTARENAS: Monteverde, 1345-1600 m (3 FMNH, 1 INBio, 24 KU, 3 LACM, 1 MMNH, 7 UMMZ); Monteverde Cloud Forest Reserve, 1530-1660 m (5 KU); San Luis [ca. 2.5 km S Monteverde], 1200 m (1 KU).

C. parva orophila (21).--COSTA RICA: ALAJUELA: Zarcero, 6000 ft (1 FMNH); CARTAGO: Cartago (1 KU, 2 UMMZ); Coliblanco (2 KU); Estrella de Cartago (1 UMMZ); Guarco (1 KU); Irazu Range (1 AMNH - holotype); La Estrella (1 AMNH). HEREDIA: Barva, San José de la Montaña, Paso Llano, 1800 m (3 KU); Barva, San Miguel de la Montaña, 1690-1700 m (3 KU). SAN JOSE: 10 mi S. of Cartago, El

Muñeco, 3800 ft (1 UMMZ); Cerro Tablazo, 1500-1983 m (1 USNM); San Rafael de Montes de Oca, 4300 ft (1 KU); Santa Ana (1 LSU); Santa Clara (1 MNCR).

GEOGRAPHIC VARIATION AND BIOGEOGRAPHICAL RELATIONSHIPS IN THE *CRYPTOTIS GOLDMANI*-*GOODWINI* COMPLEX OF SMALL-EARED SHREWS (INSECTIVORA: SORICIDAE), WITH THE DESCRIPTION OF A NEW SPECIES

Small-eared shrews of the New World genus *Cryptotis* range from southernmost Canada, through the eastern half of the United States, Mexico, and Central America, to the Andean highlands of northwestern South America. Historically, a large array of names has been proposed for the Mexican and Central American members of the genus; however, the paucity of specimens available hindered assessment of individual and geographic variation. Choate (1970), in his monograph on the Middle American members of this group, recognized eight species, which he arranged into three informal groupings: the "*C. mexicana*-group" (containing 3 species), the "*C. parva*-group" (2 species), and "relict species" (3 species). Recently, we (Woodman and Timm, 1992) described a ninth species for the region, *C. hondurensis*, from high elevation pine and mixed pine-oak forest of south central Honduras.

One of the most problematic of Choate's (1970) groups is the *C. mexicana* species group, in which he recognized

three species: C. goldmani, C. goodwini, and C. mexicana. These are high elevation shrews that occur from Tamaulipas, Mexico, to El Salvador. Members of the C. mexicana group can be recognized by the derived position of the zygomatic plate, the posterior border of which is even with the posterior border of the maxillary process or slightly posterior to the process. In all other North and Central American species of Cryptotis, as well as in Blarina and Sorex, which are considered to be the sistergroups of Cryptotis (George, 1986), the posterior border of the zygomatic plate is anterior to the posterior border of the maxillary process. Members of the C. mexicana group also have a coronoid process that joins the horizontal ramus of the mandible at a relatively wide angle, similar in some respects to that of C. gracilis (Woodman and Timm, submitted).

Cryptotis goldmani and C. goodwini are linked phylogenetically by their possession of enlarged front feet and broad claws (Fig. 20), a derived characteristic unique among members of the genus. Cryptotis goldmani, with two subspecies, C. g. alticola and C. g. goldmani, was known to range from Jalisco, Mexico, southeast into Guatemala. The monotypic C. goodwini originally was described from Guatemala (Jackson, 1933). Later, Felten (1958) reported a single specimen of C. goodwini from

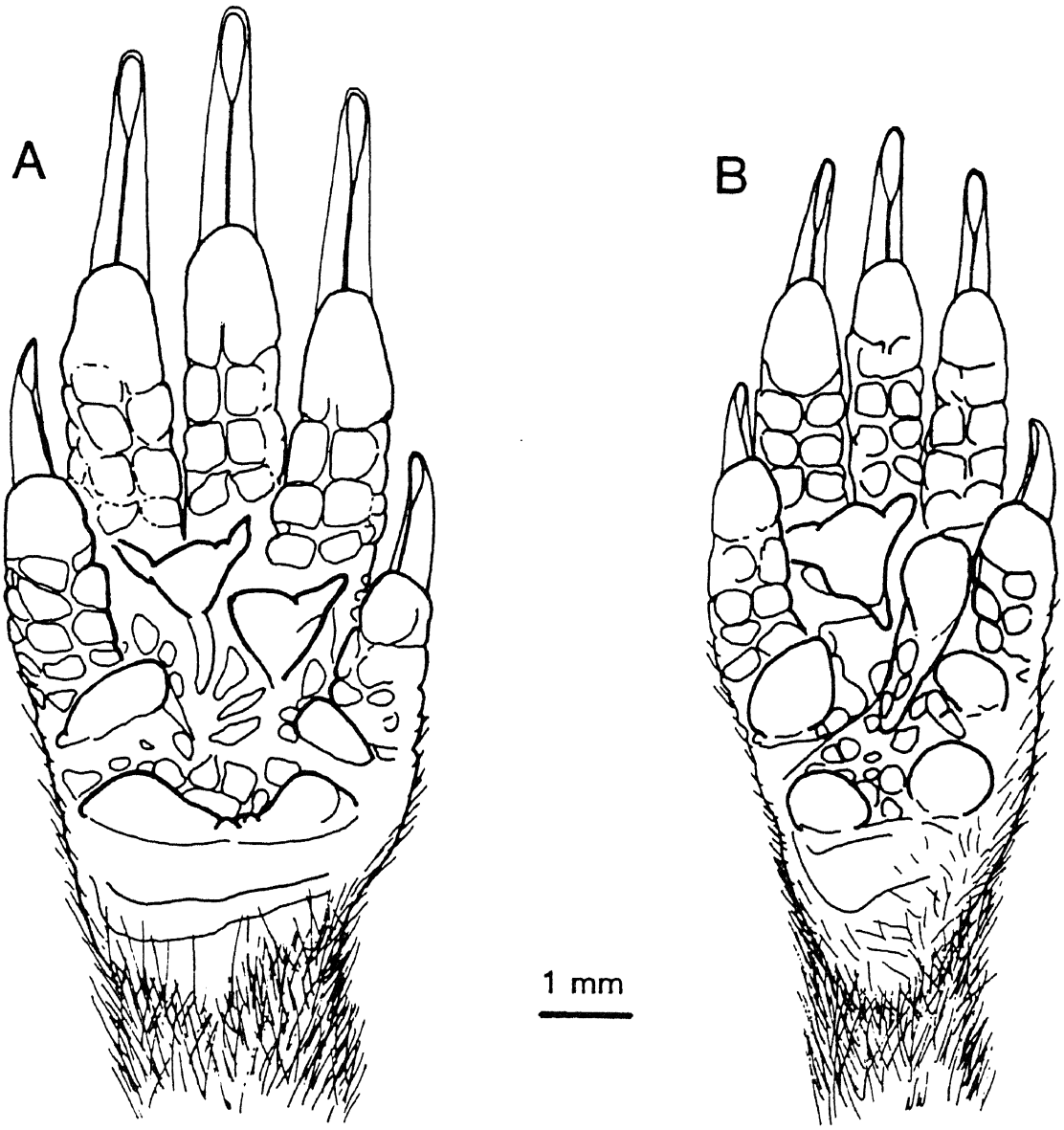

Figure 20. Ventral view of the right forefoot of C. goldmani (A; UMMZ 114710; HB = 68 mm) and C. mexicana peregrina (B; KU 124284; HB = 71 mm).

Hacienda Montecristo, in a geographically isolated area of El Salvador. This was the only record of C. goodwini from that country (Choate, 1970), but the identification of this specimen was never confirmed. Medellín (1988) recorded C. goodwini from Chiapas, thereby extending the known range of the species westward. We recently obtained a new specimen of the C. goldmani-C. goodwini complex from Honduras, which is outside of the previously known range for these shrews. Our attempts to identify this specimen and adequately document its biogeographic relationship to other large-footed Cryptotis led us to reevaluate the taxonomic status of these poorly known shrews.

It is the purpose of this paper to review our knowledge of the large-footed Cryptotis of the C. goldmani-C. goodwini complex, among which we herein recognize five distinct species. We redescribe four previously described species (C. alticola, C. goldmani, C. goodwini, and C. griseoventris) and provide a description and illustrations of one species new to science. Our analysis includes a reappraisal of the only known specimen of C. goodwini from El Salvador. We also review the available information on reproduction, elevational distributions, and habitat for these five species, and we provide a key for their identification.

Methods

Cranial and mandibular measurements were taken to the nearest 0.1 mm using either an ocular micrometer in a binocular microscope or a hand-held dial caliper. Skin measurements are those recorded by the collector, except for head and body length, which we calculated by subtracting the recorded tail length from the total length. All measurements are in millimeters. Univariate statistics include mean ± standard deviation. Terminology of dental characteristics follows Choate (1970). We also follow Choate (1970) in referring to the upper dentition between the incisor and P4 as unicuspids, abbreviated U1, U2, etc. The measurements used in our analyses follow Woodman and Timm (submitted). These include: head and body length (HB); tail length (TL); condylobasal length (CBL), not including the upper incisors; cranial breadth (CB); breadth of zygomatic plate (ZP); interorbital breadth (IO); breadth of palate across first unicuspids (U1B); breadth of palate across third unicuspids (U3B); breadth of palate across second molars (M2B); palatal length (PL); upper toothrow length, U1 to M3, parallel to the long axis of the skull (TR); unicuspid toothrow length, parallel to the unicuspid toothrow (UTR); molariform toothrow, P4 to M3, parallel to long axis of the skull

(MTR); mandibular length, from deepest point of inferior sigmoid notch to posterior edge of mental foramen (ML); height of coronoid process (HCP); height of coronoid valley (HCV); height of articular condyle (HAC); breadth of articular condyle (BAC); distance from articular condyle to posterior edge of m3 (AC3); lower toothrow length (TRD). All capitalized color names follow Ridgeway (1912). Localities and elevations that we report are taken directly from specimen tags and represent the descriptions of the original collectors. We provide corrections and additions in brackets. Additional information on specimens collected by E. W. Nelson and E. A. Goldman was obtained from Goldman (1951). Distances measured in miles or elevations measured in feet are not converted to metric measures to avoid inferring a level of accuracy greater than that originally recorded by the collector.

Multivariate analyses were carried out using BMDP on the University of Kansas Academic Computing Services' IBM 3031AP processor running a VM/CMS computer system.

Sexual dimorphism in Cryptotis was investigated previously for C. mexicana (Choate, 1970) and C. gracilis (Woodman and Timm, submitted). Neither study demonstrated evidence of any clear, overall pattern of variation between sexes, although each study identified

an individual variable that was statistically different between males and females. In addition, we (Woodman and Timm, submitted) documented that geographic variation was a more important component of overall variation in C. gracilis than sexual variation. In the present study there were insufficient sample sizes of complete individuals of both sexes to carry out adequate analyses of secondary sexual variation for any species. Based on lack of obvious sexual variation in other members of the genus, we assumed that there was no compounding sexual variation in our analyses. Males, females, and specimens of unknown sex were combined in all analyses.

Comparisons of character state distributions among specimens examined led us to recognize four distinct groups, which we consider to be definable species. From this analysis we further determined that the single specimen from Honduras is distinct from each of the other four groups. The occurrence of C. goodwini in an isolated area in El Salvador is based on a single specimen (Felten, 1958; Choate, 1970). This singleton from El Salvador could not be separated from other C. goodwini on more than a single character. In order to determine whether the four recognized groups and the specimens from El Salvador and Honduras could be distinguished on the basis of combined mensural

characteristics, principal components analysis (PCA) was carried out using 10 variables (CBL, ZB, PO, U1B, U3B, M2B, PL, TR, UTR, MTR) on 74 specimens: 16 C. alticola, 16 C. goldmani, 20 C. goodwini, 20 C. griseoventris, and the single specimens from El Salvador and Honduras.

In a further attempt to distinguish among groups, discriminant function analyses (DFA) were performed using the same 10 variables as were used for PCA. The singletons from El Salvador and Honduras were added to the discriminant function model as unknowns to determine where they would plot in relation to the four known groups. A protected F-to-enter (α = 0.05/10 comparisons = 0.005) was used for this analysis because of the multiple comparisons among groups.

Specimens from the following institutions were used in this study: American Museum of Natural History, New York (AMNH); Angelo State University Natural History Collection, San Angelo (ASNHC); California Academy of Sciences, San Francisco (CAS); Escuela Nacional de Ciencias Biológicas, Mexico City (ENCB); Field Museum of Natural History, Chicago (FMNH); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (IBUNAM); University of Kansas Museum of Natural History, Lawrence (KU); Los Angeles County Museum of Natural History, Los Angeles (LACM); Museum of

Comparative Zoology, Harvard University, Cambridge (MCZ); James Ford Bell Museum of Natural History, Minneapolis (MMNH); Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City (MZFC); Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF); Texas Cooperative Wildlife Collection, College Station (TCWC); Universidad Autónoma Metropolitana Iztapalapa, Mexico City (UAMI); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); US National Museum, Washington (USNM).

Results

Multivariate analyses confirmed the a priori definition of the four groups of Cryptotis. A plot of factor 1 scores vs. factor 2 scores from PCA separated the four groups that we herein recognize as species, generally with a minimum of overlap (Fig. 21). All variables, with the exception of ZP, weighted heavily on factor axis 1, indicating that it is a good measure of overall size. Factor axis 2 is a contrast between UTR and a negatively weighted combination of U1B and M2B. The specimen from El Salvador plots out between C. alticola and C. goodwini, where it defines the lower limit of C. goodwini on factor axis 2. The Honduran specimen plots out near the center of the graph in an

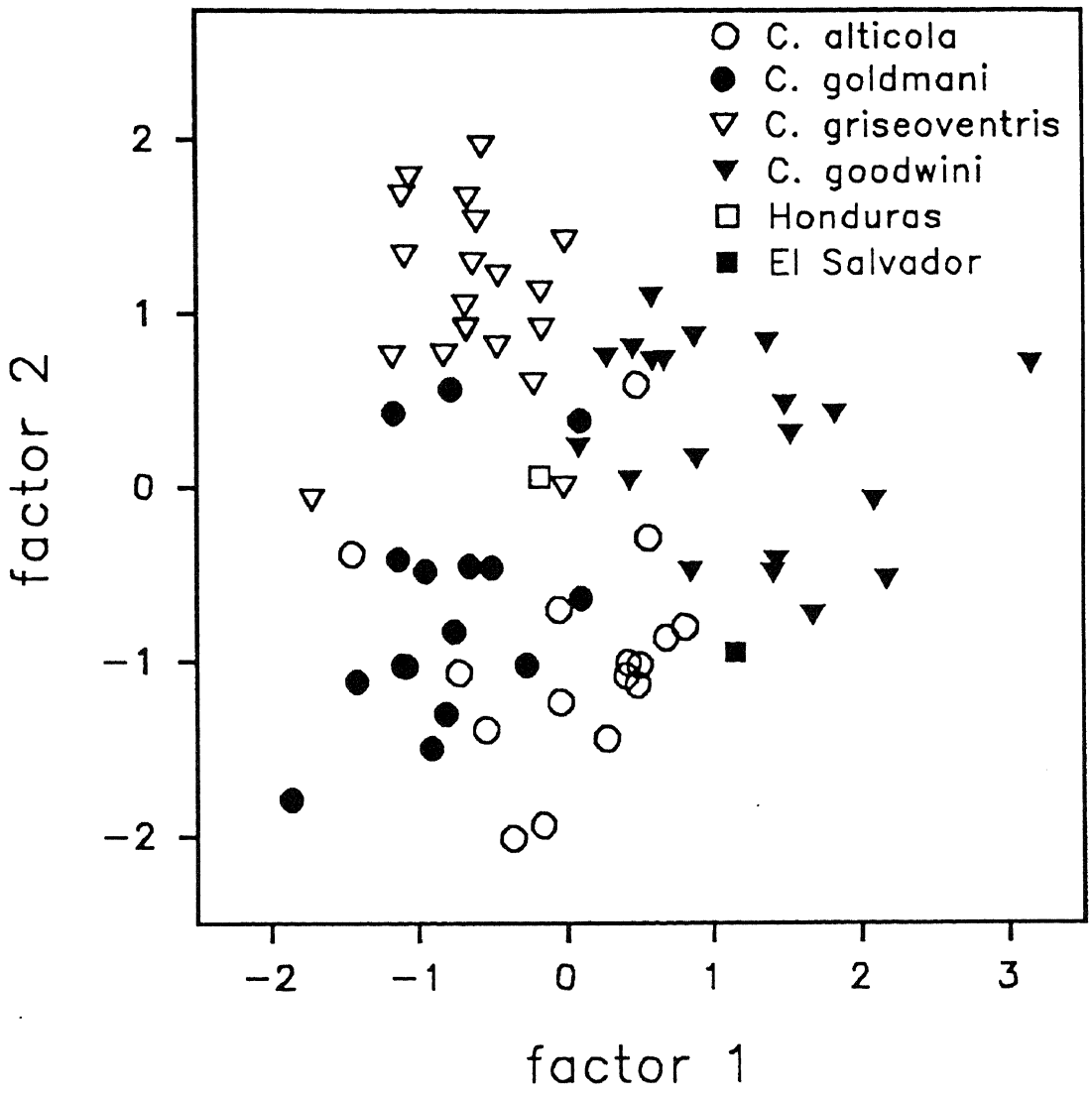

Figure 21. Plot of specimens of C. alticola, C. goldmani, C. goodwini, C. griseoventris, and the Honduran specimen on PCA factor axes 1 and 2.

area of overlap among extremes of C. goldmani, C. griseoventris, and C. goodwini, indicating that it is intermediate among these groups on factor axes 1 and 2. Two specimens of C. alticola plotted well away from other members of their species; one specimen (UMMZ 93367) from Santa Rosa, Mexico, has a long, narrow skull and plotted out on the graph in an area dominated by C. goodwini. The other is one of a pair of specimens from Lagunas de Zempoala, Mexico (USNM 329424). The deviant specimen has a particularly narrow palate and small mandibular measurements, and it plotted in an area dominated by C. goldmani. This specimen defines the lower limit of many cranial variables for C. alticola, yet it is fairly normal in size for HB, TL, and CBL.

The DFA model utilized four variables (M2B, UTR, IO, MTR), which provide clear separation among all four groups with little overlap (Fig. 22). Canonical axis 1 separated C. goodwini and C. griseoventris from C. alticola and C. goldmani, and canonical axis 2 separated C. goodwini and C. alticola from C. griseoventris and C. goldmani. There were only two misclassifications: one C. alticola (USNM 329424) was identified as C. goldmani, and a C. goldmani from Omiltemi (KU 98725) was classified as C. alticola. The El Salvadoran specimen, entered as an unknown, was classified as C. goodwini.

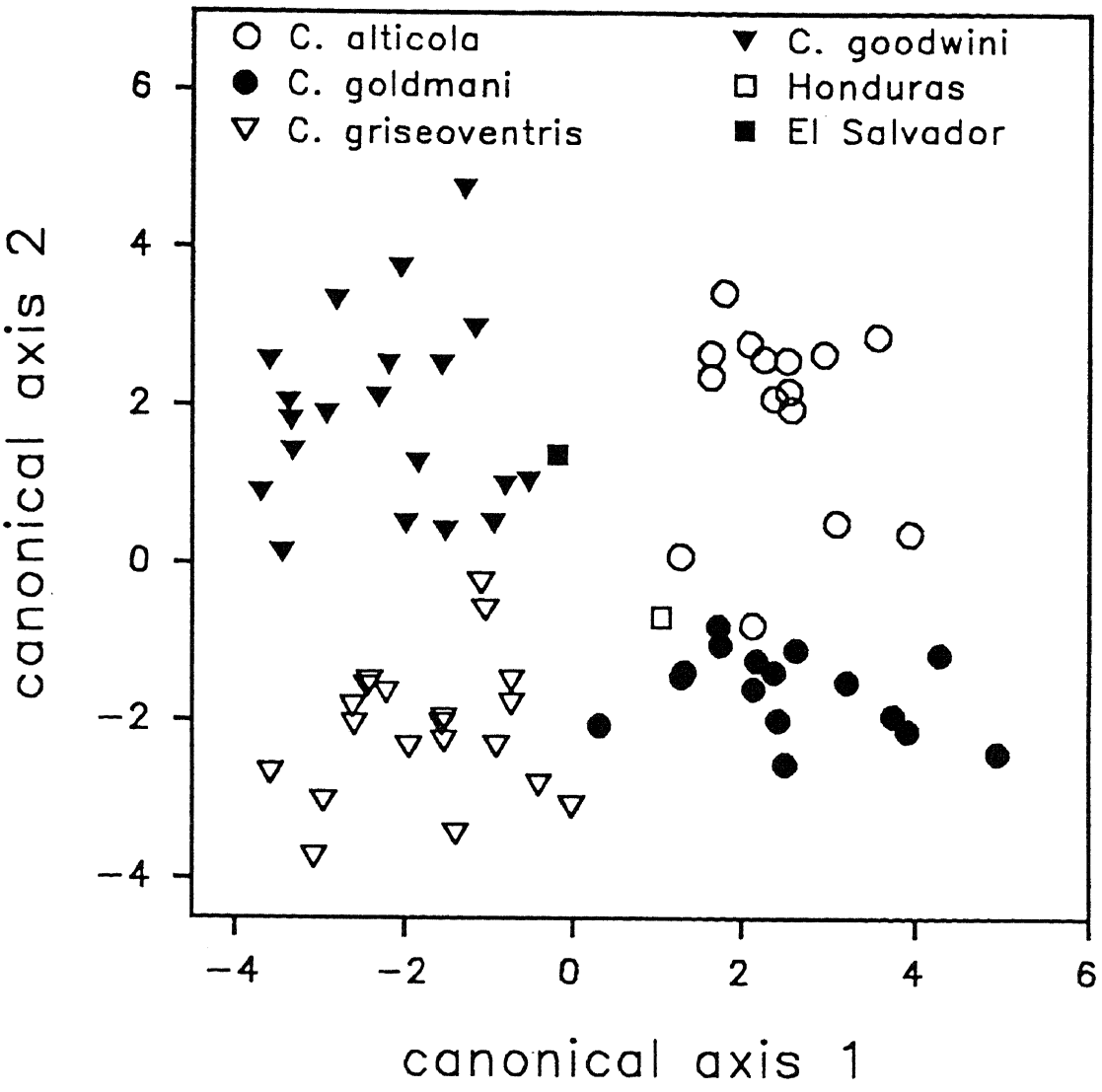

Figure 22. Plot of specimens of C. alticola, C. goldmani, C. goodwini, C. griseoventris, and the Honduran specimen on DFA canonical axes 1 and 2.

The Cryptotis from Honduras was classified as C. goldmani, but plots on the periphery of this group.

Discussion

Based on elevational and geographic distributions of specimens (Fig. 23) and the correlation of character states to these elevational and geographic distributions, we recognize five distinct species among the large-footed shrews previously placed in C. goldmani and C. goodwini: C. alticola, C. goldmani, C. goodwini, C. griseoventris, and one species new to science. Recognition of five species is supported further by our ability to separate the taxa using multivariate analyses. We consider C. alticola, which inhabits highlands in central Mexico, to be a distinct species. The populations known as alticola were described originally as a distinct species (Merriam, 1895). Choate (1970), who first revised these taxa, considered them to be "incipient species", but treated them formally as subspecies. The ranges of these two taxa are completely separate, and there is no evidence of intergradation. Cryptotis alticola differs from C. goldmani in its larger average size, shorter tail, and much broader palate. In addition, specimens of C. goldmani from the states of Guerrero and Oaxaca possess a well developed foramen posterior to the external

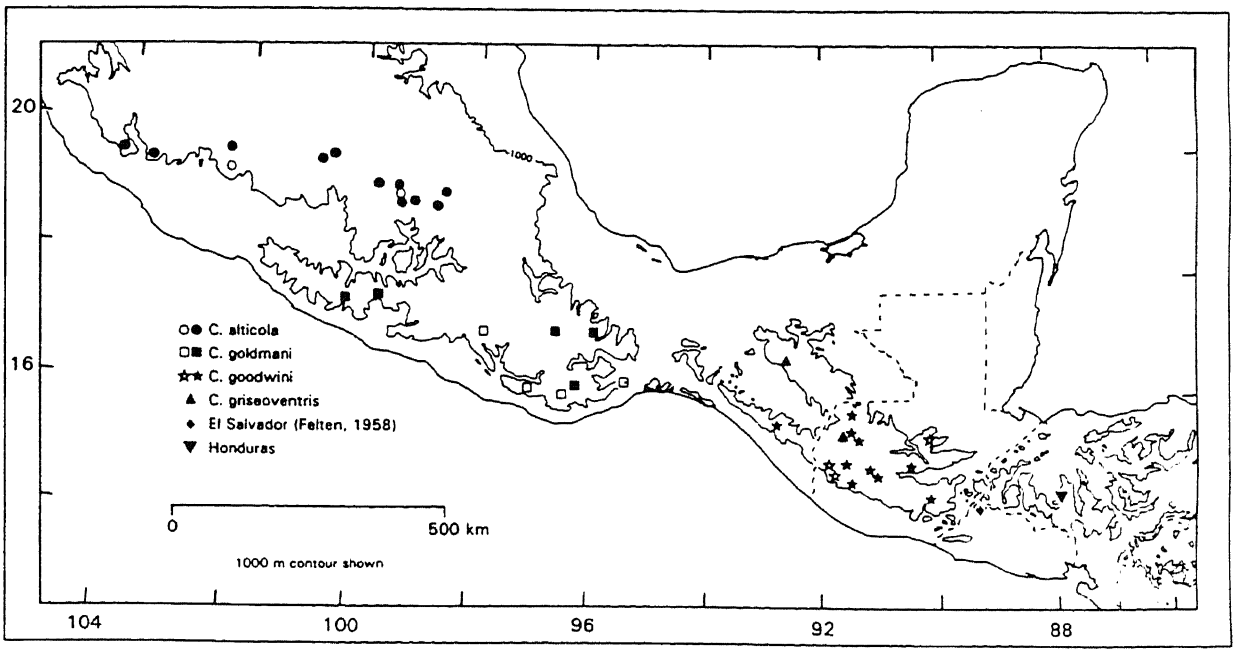

Figure 23. Map of southern Mexico and northern Central America indicating the distribution of the species in this study. Solid symbols represent localities from which specimens were examined in this study; open symbols are records from the literature. Contours represent 1000 m elevation.

capitular facet (sensu McDowell, 1958). This foramen (Fig. 24) is present on one or both sides of the skull in fewer than 60% of C. alticola, and, when present, it is always minute and never well developed. Specimens previously identified as C. goldmani goldmani (Choate, 1970) from the Mexican State of Chiapas and from Guatemala lack the foramen posterior to the external capitular facet. In addition the unicuspid toothrow is relatively and absolutely longer in these specimens than in C. goldmani from Guerrero and Chiapas, and their geographic ranges are not conterminous. For these reasons, we restrict the name C. goldmani to those specimens from Guerrero and Chiapas. We refer the specimens from Chiapas and Guatemala to the species C. griseoventris Jackson. Cryptotis griseoventris was described by Jackson (1933) as a species, but later was considered a junior synonym of C. goldmani goldmani (Choate, 1970; Hall, 1981). The geographic range of C. griseoventris overlaps that of C. goodwini, from which it can be distinguished by C. goodwini's much larger size.

The specimen from El Salvador is similar in size and most cranial characteristics to C. goodwini, differing from that species only in having much less emarginate upper dentition. Multivariate analyses support previous

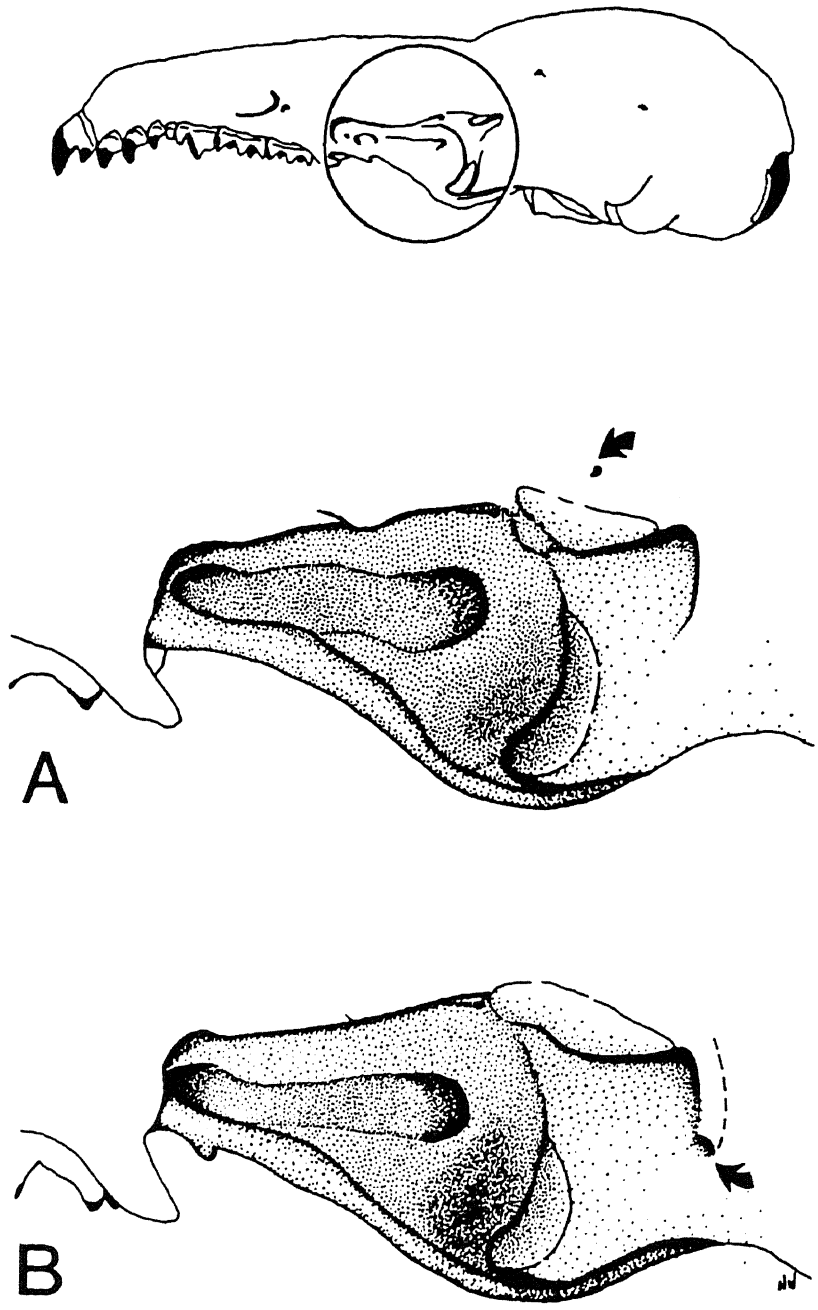

Figure 24. Lateral view of the orbital area of the skulls of C. griseoventris (A; USNM 75887) and C. goldmani (B; KU 98727) indicating locations of the foramina dorsal to (A) and posterior to (B) the external capitular facet. Dashed line on B indicates the path of the ventral branch of the sinus canal.

identifications of the specimen from El Salvador as C. goodwini. However, the highland area from which this shrew was collected is isolated geographically from highlands occupied by C. goodwini by the deep valley of a tributary of the Río Chioquimula. It is further isolated by deep valleys from the highland areas conterminous with the Cerro de Montecillos, from which the Honduran specimen was collected. We suspect that further analysis of a larger series of specimens from this region would show that it represents a distinct species. We refer it to C. goodwini as the best available name for it at this time.

The specimen from Honduras has a much longer zygomatic plate than is found in any other species of large-footed shrew, and it differs from its nearest neighbors, C. goodwini and C. griseoventris, in its relatively and absolutely shorter tail. This shrew can not be referred to any previously described species, and we describe it below as a species new to science.

Species Accounts

Cryptotis alticola

Blarina alticola.--Merriam, 31 December 1895, N. Amer. Fauna 10:27.

Cryptotis alticola.--Miller, 31 December 1912, Bull.

U.S. Natl. Mus. 79:27; Davis, 12 December 1944, J. Mammal. 25:376; Hooper, 30 April 1957, Univ. Michigan Mus. Zool. Occas. Papers 586:3; Hall and Kelson, 31 March 1959, The Mammals of North America 1:60; Genoways and Choate, 1 December 1967, Proc. Biol. Soc. Washington 80:204.

Cryptotis euryrhynchis.--Genoways and Choate, 1 December 1967, Proc. Biol. Soc. Washington 80:203.

Cryptotis goldmani alticola.--Choate, 30 December 1970, Univ. Kansas Pub. Mus. Nat. Hist. 19:245; Hall, 3 April 1981, The Mammals of North America 1:59.

Holotype.--Skin and skull of adult male, USNM 52047; collected 25 February 1893 by E. W. Nelson (collector number 4396); from Mexico, State of Mexico, Volcán Popocatépetl, 11,500 ft.

Distribution.--Highland areas over 2000 m in the Mexican states of Jalisco, Michoacan, Mexico, and Puebla, and the Distrito Federal.

Description.--Size medium for the genus (Table 5); tail short, averaging 26 mm, or ca. 33% of head and body length; front feet large and claws broad; dorsal guard

Table 5. Skin measurements of Cryptotis used in this study. Abbreviations of measurements are explained in Methods section of text. Number of individuals used for each species is given in parentheses. The statistics presented are mean ± standard deviation of the mean and the observed extremes.

	HB	TL	TL/HB (%)
C. alticola	(22)		
	79 ± 5	26 ± 2	33 ± 4
	69 - 87	23 - 30	27 - 41
C. goldmani	(28)		
	76 ± 5	29 ± 3	38 ± 5
	62 - 84	24 - 36	31 - 48
C. goodwini	(34)		
	84 ± 5	29 ± 2	35 ± 3
	75 - 94	25 - 34	30 - 41
C. griseoventris	(27)		
	77 ± 3	29 ± 1	38 ± 2
	73 - 85	27 - 32	34 - 42
Cryptotis "C"	(1)		
	80	25	31

hairs about 6-8 mm long; dorsal pelage Olive Brown/Mummy Brown/Bister/Clove Brown; venter somewhat lighter, Light Grayish Olive/Drab/Buffy Brown to Olive Brown; dorsal fur distinctly three-banded: basal 5/6ths of hairs silvery gray, followed by a thin, lightly colored band, grading abruptly to the brownish tip.

Rostrum of normal length (PL/CBL = 43.2% ± 1.2, n = 16) for Cryptotis; more than half of specimens examined (57%, n = 21) have two well developed dorsal foramina near suture between the frontals (= foramina orbitalia of Bühler, 1964); a minute ventral extension of the sinus canal may be present posterior to the external capitular facet on one (29%, n = 14) or both (29%) sides of the skull (see comments under account for C. goldmani); zygomatic plate not elongate (ZP/PL = 21.8%, n = 16), anterior border aligned with mesostyle-metastyle valley of M1, posterior border normally aligned with posterior base of maxillary process; palate wide; upper toothrow uncrowded, U4 aligned with toothrow and partly visible in labial view; P4, M1, M2 slightly to moderately recessed on posterior border, emargination reaching about halfway to hypocone; M3 with paracrista, paracone, and precentrocrista, as well as small, lightly colored or uncolored protocone; mesostyle of M3 normally is small and uncolored, and sometimes there is a short,

uncolored postcentrocrista; hypocone on M3 is absent or poorly developed; dentition not bulbous.

Mandible relatively long and of moderate breadth; coronoid process joins horizontal ramus at a relatively wide angle; distance between coronoid process and posterior border of m3 is long; viewed posteriorly, articular process generally tall and moderately wide, with a moderately broad articular facet; lower sigmoid notch deep; posterior border of lower incisor extends to posterior cingulum of p4; entoconid of m3 normally present, but very reduced (69%, n = 13), or it may be absent (31%).

Comparisons.--Comparisons of C. alticola with other members of the complex are presented under accounts for those species. Selected measurements are presented in tables 1 and 2.

Remarks.--Choate (1970) noted many of the differences between C. alticola and C. goldmani and considered C. alticola to possess a greater number of derived features, particularly in the dentition. Choate (1970:244) termed C. alticola an "incipient species", but treated it formally as a subspecies of C. goldmani. Our analysis demonstrates that the taxon warrants recognition as a species.

Cryptotis alticola generally has a relatively simple M3 morphology. However, a few specimens exhibit a more complex M3, with a well developed mesostyle, postcentrocrista, and protocone, and a vestigial hypocone. A male from a series collected at Lagunas de Zempoala (USNM 329426) has a complex M3, although other specimens from this locality have a simple M3 more typical of the species. A male specimen from 12 mi W Ciudad Hidalgo (KU 66280) also has a complex M3.

Few reproductive data are available for C. alticola. A female from 12 km ESE Amecameca was lactating on 15 June (KU 17691), and a pregnant female was found dead along a trail on Sierra Patamba on 1 July (KU 62311). Study skins that we inspected had well-developed lateral glands on 3 males collected 21-25 March, 2 of 3 males collected on 27-28 April, and 3 males collected in June. Lateral glands were not visible on males captured in January (n = 1), February (1), July (1), or October (1). On study skins lateral glands appear as paired, oval areas about 6-9 mm in length and 5-6 mm in width. These glandular areas lack long guard hairs or normal underfur, but have a sparse covering of short, fine, lightly colored hairs. No specimens identified as females in our study had well developed lateral glands. Among most genera of Soricidae, both males and females

possess lateral glands, but those of females are smaller and more difficult to see (Murariu, 1976; Bee et al., 1980). Eadie (1938) found that the lateral glands of Blarina showed increased activity with enlargement of the testes, and it seems likely that they may serve a function in sexual and social communication.

Cryptotis alticola is known to occur in high-elevation forests dominated by pines (Pinus) and often mixed with fir (Abies), oaks (Quercus), and other tree species. At least some of the areas inhabited by C. alticola are subjected to winter frosts and occasional snow (Goldman, 1951). Percy L. Clifton noted [field notes - KU] that he collected three shrews on the relatively dry east side of a hill in an area of bunch grass under scattered pine, oak, and fir at 9000 ft 20 mi SE Autlán on 27-28 April 1967. The moister western slope of the hill supported denser forest. He collected three additional Cryptotis alticola in Museum Special snap traps set along the same rotten log in a grassy area along the edge of a fir, pine, and hemlock forest at 10,000 ft 12 mi SW Ciudad Guzmán on 11 June 1967. Walter W. Dalquest recorded [field notes - KU] having caught this species, along with Microtus mexicanus, Neotomodon alstoni, Peromyscus melanotis, and Reithrodontomys chrysopsis, in a clearing dominated by

three-foot-high clumps of sacatón grass in coniferous forest at 11,500 ft 12 km ESE Amecameca on 14-15 June 1946.

Cryptotis goldmani

Blarina mexicana goldmani.--Merriam, 31 December 1895, N. Amer. Fauna 10:25.

Blarina mexicana machetes.--Merriam, 31 December 1895, N. Amer. Fauna 10:26.

Blarina fossor.--Merriam, 31 December 1895, N. Amer. Fauna 10:28.

Cryptotis frontalis.--Miller, 31 October 1911, Proc. Biol. Soc. Washington 24:222; Hall and Kelson, 31 March 1959, The Mammals of North America 1:60; Goodwin, 30 April 1969, Bull. Amer. Mus. Nat. Hist. 141:40.

Cryptotis mexicana goldmani.--Miller, 31 December 1912, Bull. U.S. Natl. Mus. 79:27; Davis and Lukens, 20 August 1958, J. Mammal. 39:350; Hall and Kelson, 31 March 1959, The Mammals of North America 1:59; Genoways and Choate, 1 December 1967, Proc. Biol. Soc. Washington 80:204.

Cryptotis mexicana machetes.--Miller, 31 December 1912,

Bull. U.S. Natl. Mus. 79:27; Hall and Kelson, 31 March 1959, The Mammals of North America 1:60; Schaldach, October 1966, Säugetierkd. Mitt. 14:288; Goodwin, 30 April 1969, Bull. Amer. Mus. Nat. Hist. 141:40 (in part).

Cryptotis fossor.--Miller, 31 December 1912, Bull. U.S. Natl. Mus. 79:27; Hall and Kelson, 31 March 1959, The Mammals of North America 1:62; Goodwin, 30 April 1969, Bull. Amer. Mus. Nat. Hist. 141:41.

Cryptotis guerrerensis.--Jackson, 27 April 1933, Proc. Biol. Soc. Washington 46:80; Hall and Kelson, 31 March 1959, The Mammals of North America 1:60.

Notiosorex phillipsii.--Goodwin, 30 April 1969, Bull. Amer. Mus. Nat. Hist. 141:43 (in part).

Cryptotis mexicana mexicana.--Jones and Genoways, 20 May 1967, J. Mammal. 48:321; Goodwin, 30 April 1969, Bull. Amer. Mus. Nat. Hist. 141:39 (in part).

Cryptotis goldmani goldmani.--Choate, 30 December 1970; Univ. Kansas Pub. Mus. Nat. Hist. 19:247 (in part); Hall, 3 April 1981, The Mammals of North America 1:59 (in part).

Holotype.--Skin and skull of adult male, USNM 70244; collected 23 December 1894 by E. W. Nelson and E. A. Goldman (collector number 7231); from Mexico, Guerrero, mountains near Chilpancingo, 9600 ft.

Distribution.--Conterminous high mountain areas in the Sierra Madre del Sur and Sierra Madre de Oaxaca; found above 1500 m in the Mexican state of Guerrero and above 2000 m in Oaxaca.

Description.--Size medium for the genus (Table 5); tail moderately long, averaging 29 mm, or ca. 38% of head and body length; front feet enlarged and claws broad; dorsal guard hairs normally about 6-8 mm long; dorsal pelage Mummy Brown; ventral pelage somewhat lighter than dorsum, between Light Drab and Drab; dorsal fur three-banded: basal 5/6ths of hairs silvery gray, followed by a thin, lightly colored band, grading into brown tip.

Rostrum of normal length (PL/CBL = 44.2% $\pm$ 1.0, n = 16) for Cryptotis; often (48%, n = 23) two well developed dorsal foramina; a well developed foramen leading to a ventral extension of the sinus canal typically present posterior to the external capitular facet (i.e., the upper articular surface of the glenoid fossa) on one (4.5%, n = 22) or both (91%) sides of the skull; zygomatic plate not elongate (ZP/PL = 21.2%, n =

16), anterior border usually aligned with mesostyle-metastyle valley of M1, but may extend as far posterior as parastyle M2; posterior border of zygomatic plate aligned with posterior base of maxillary process; upper toothrow uncrowded, U4 aligned with toothrow and usually partly visible in labial view; P4, M1, M2 only very slightly recessed on posterior border; M3 with paracrista, paracone, and precentrocrista, as well as small, lightly pigmented or unpigmented protocone; mesostyle of M3 normally is small and uncolored, and occasionally there is a short, uncolored postcentrocrista; hypocone on M3 is absent or poorly developed; dentition not bulbous.

Mandible of moderate length and breadth; coronoid process joins horizontal ramus at a relatively wide angle; distance between coronoid process and posterior border of m3 is long; articular process tends to be tall and wide, with a narrow ventral articular facet and a shallow lingual notch between articular facets (Oaxaca), or tall and moderately wide, with a broad ventral articular facet and a deep notch between articular facets (Guerrero); lower sigmoid notch deep; posterior border of lower incisor extends to posterior cingulum of p4; entoconid of m3 normally absent (40%, n = 20) or poorly-developed (55%), occasionally well developed

(5%).

Comparisons.--Cryptotis goldmani is the only member of the C. mexicana species group with a well developed foramen posterior to the external capitular facet.

Cryptotis alticola.--Cryptotis goldmani averages somewhat smaller in HB and CBL, and has a relatively and absolutely longer tail; much narrower palate; P4, M1-2 only very slightly recessed posteriorly; shorter mandible.

Remarks.--Cryptotis goldmani is unique among the large-footed Cryptotis in its possession of a well developed ventral extension of the sinus canal (Fig. 24B). This branch of the sinus canal lies posterior to the external capitular facet and exits through a foramen approximately the size of the anterior orifice of the sinus canal (sensu McDowell, 1958). This ventral branch of the sinus canal is absent from all specimens of C. griseoventris and C. goodwini that we have inspected, and also from the specimens from El Salvador and Honduras. There is a minute foramen associated with an equally tiny ventral branch of the sinus canal developed on one or both sides of the skull in most C. alticola (58%, n = 14). Minute ventral foramina also are present in C. mexicana mexicana (47%, n = 30), C. mexicana

peregrina (2 of 3), and C. mexicana obscura (3 of 7); the ventral foramina are similar to those in C. alticola, but never are as large as in C. goldmani.

Most Blarina (56 of 60 specimens of B. brevicauda, B. carolinensis, and B. hylophaga) have a foramen dorsal to the external capitular facet (Fig. 24A) on one (5) or both (51) sides of the skull. Typically this foramen is well developed, about the size of the anterior orifice of the sinus canal, and easily seen. In Cryptotis the presence of this foramen is highly variable, both within and among species. When present, the foramen may be well developed and obvious or minute and very difficult to see. Among C. alticola a foramen is present on one or both sides of the skull in 59% of the specimens we examined (n = 17). This foramen also is present in 46% of Cryptotis goldmani (n = 22), 96% of C. griseoventris (n = 25), and 95% of C. goodwini (n = 19). Among the large-footed Cryptotis the foramen dorsal to the external capitular facet is much less prevalent in those species which usually have a ventral branch of the sinus canal.

Cryptotis mexicana mexicana from Oaxaca often have long claws on their forefeet, making them difficult to distinguish from C. goldmani. Although the claws of C. mexicana mexicana normally are not as broad as those of

C. goldmani, this character is difficult to use without specimens of both in hand, and even then, large C. mexicana and small C. goldmani are difficult to differentiate. Cryptotis goldmani tends to be larger (HB = 75; CBL = 19.6; see Tables 5 and 6) than Oaxacan C. mexicana mexicana (HB = 67 ± 3, n = 16; CBL = 18.6 ± 0.4, n = 13), but again the two species overlap. Cryptotis goldmani can be best identified by a combination of cranial characteristics; they nearly always have a well developed foramen leading to the ventral extension of the sinus canal, and the entoconid on m3 is reduced or absent. In contrast, although the foramen of the ventral branch is usually present (58%, n = 19) on one or both sides of the skull in Oaxacan C. mexicana mexicana, it is always minute, and never approaches the size of that in C. goldmani. In C. mexicana mexicana the entoconid of m3 is always well developed (100%, n = 19), although it often is not pigmented.

Reproductive data for C. goldmani are lacking. Our examination of lateral glands on preserved study skins reveals a pattern similar to that of C. alticola; lateral glands were well developed in 3 males collected 21-25 March, 2 of 3 from 27-28 April, 3 males from 11-15 June, 4 males from 25-26 July, and one male from 5

Table 6. Cranial and mandibular measurements of Cryptotis used in this study. Abbreviations of measurements are explained in Methods section of text. Number of individuals is given in parentheses. The statistics presented are mean ± standard deviation of the mean, and observed extremes.

Table 6

	C. alticola (16)	C. goldmani (16)	C. goodwini (20)	C. griseoventris (20)	Cryptotis "C" (1)
CBL	20.2 ± 0.5 19.3 - 21.1	19.6 ± 0.5 18.9 - 20.5	21.1 ± 0.7 20.0 - 22.8	19.9 ± 0.4 18.8 - 20.4	20.3
CB	10.4 ± 0.2 9.9 - 10.8 (15)	10.2 ± 0.2 9.8 - 10.5 (18)	11.1 ± 0.3 10.6 - 11.6 (15)	10.2 ± 0.2 9.8 - 10.7 (19)	10.8
ZP	1.9 ± 0.1 1.7 - 2.1	1.8 ± 0.2 1.4 - 2.2	1.9 ± 0.1 1.6 - 2.2	1.9 ± 0.1 1.6 - 2.1	2.2
IO	4.9 ± 0.2 4.7 - 5.3	5.0 ± 0.2 4.7 - 5.3	5.6 ± 0.2 5.3 - 5.8	5.1 ± 0.2 4.8 - 5.3	5.3
U1B	2.7 ± 0.1 2.5 - 2.8	2.6 ± 0.1 2.4 - 2.7	2.7 ± 0.1 2.6 - 2.9	2.5 ± 0.1 2.3 - 2.6	2.6
U3B	3.2 ± 0.1 3.0 - 3.2	3.0 ± 0.1 2.8 - 3.2	3.3 ± 0.1 3.0 - 3.5	3.0 ± 0.1 2.8 - 3.2	3.0
M2B	6.2 ± 0.2 5.8 - 6.4	5.8 ± 0.1 5.6 - 5.8	6.2 ± 0.2 6.0 - 6.6	5.6 ± 0.1 5.4 - 5.9	5.9
PL	8.7 ± 0.3 8.1 - 9.2	8.7 ± 0.3 8.0 - 9.2	9.2 ± 0.3 8.8 - 10.1	8.7 ± 0.2 8.1 - 9.0	8.8
TR	7.6 ± 0.2 7.1 - 7.9	7.4 ± 0.2 7.0 - 7.8	7.9 ± 0.3 7.5 - 8.6	7.6 ± 0.2 7.3 - 7.8	7.5
UTR	2.5 ± 0.1 2.3 - 2.7	2.3 ± 0.1 2.0 - 2.5	2.7 ± 0.1 2.5 - 2.9	2.7 ± 0.1 2.5 - 2.9	2.4
MTR	5.5 ± 0.2 5.1 - 5.7	5.4 ± 0.1 5.3 - 5.7	5.6 ± 0.2 5.3 - 5.9	5.2 ± 0.1 5.0 - 5.4	5.5
LM	6.6 ± 0.2 5.9 - 6.8	6.3 ± 0.3 5.8 - 6.8	6.6 ± 0.2 6.2 - 6.8	6.2 ± 0.2 5.7 - 6.4	6.5
HCP	4.6 ± 0.2 4.3 - 4.9	4.6 ± 0.2 4.3 - 4.9	4.8 ± 0.1 4.6 - 5.2	4.4 ± 0.1 4.2 - 4.6	4.7
HAC	4.1 ± 0.2 3.7 - 4.3	3.9 ± 0.2 3.8 - 4.2	4.2 ± 0.2 3.8 - 4.6	3.9 ± 0.1 3.7 - 4.1	4.1
BAP	3.3 ± 0.1 3.0 - 3.5	3.1 ± 0.1 2.9 - 3.2	3.3 ± 0.2 3.0 - 3.6	3.0 ± 0.1 2.8 - 3.1	3.1
AC3	5.2 ± 0.2 4.8 - 5.6	5.1 ± 0.2 4.8 - 5.3	5.6 ± 0.2 5.2 - 5.9	5.1 ± 0.1 4.8 - 5.3	5.3
TRD	6.2 ± 0.2 5.8 - 6.5	6.1 ± 0.2 5.4 - 6.4	6.4 ± 0.2 6.1 - 6.8	6.1 ± 0.1 5.8 - 6.3	5.9
HAV	2.9 ± 0.1 2.8 - 3.1	2.8 ± 0.1 2.7 - 3.0	3.0 ± 0.1 2.8 - 3.4	2.8 ± 0.1 2.6 - 3.0	2.9

August. A male from 26 December had lateral glands that were visible, but not particularly well developed. Lateral glands were not developed in single specimens from the months of January, February, and October.

Specimens of C. goldmani have been taken in high elevation pine forest and possibly oak forest in Oaxaca, and in pine forest in Guerrero. The climate of some localities where the species has been found includes severe winter frosts and heavy summer rains (Goldman, 1951). Percy L. Clifton's field notes [KU] indicate that he collected three C. goldmani in Museum Special snap traps set under rocks and logs in pine forest with scattered oak at 7300 ft at Omiltemi on 14-15 July 1964. Paul B. Robertson collected one of these shrews at 2300 m at Campemento Río Molino on 8 December 1969, and two additional specimens on 14 April 1970. Musser (1964) reported that the canyon bottom at Campemento Río Molino was relatively moist, open forest with bromeliad-covered oaks and a dense understory of shrubs, ferns and herbaceous vegetation. The higher slopes of the canyon were drier, and covered with secondary oak and pine forest.

Choate (1970:249) reported two specimens of C. goldmani from ca. 500 m at Mixteguilla and another from ca. 500 m "near the City of Tehuantepec". As far as we

could determine, no elevation or more specific locality is associated with these specimens. The lower elevational range of C. goldmani reaches almost to 1500 m in Guerrero, but nowhere in Oaxaca has it been recorded from below 2000 m. It seems most likely, given the normal environmental associations of C. goldmani, that these specimens were collected in high elevation pine forest in the general vicinity of the aforementioned towns. The lower elevational limit of C. goldmani probably varies, depending upon local environmental characteristics, but it probably nowhere reaches 500 m.

We concur with Choate (1970) that it is unlikely that there is intergradation between C. alticola and C. goldmani. There is a straight line distance of approximately 230 km between the nearest known localities for the two species. Both are high elevation species, and the only possible connection between the two ranges would be along a divide that dips to just above 1500 m where it crosses the Puebla/Oaxaca border. However, Cryptotis alticola has not been recorded from below 2000 m, which is also the lower limit for C. goldmani in most of Oaxaca, so the two shrews appear to be separated by elevational and concordant ecological barriers.

Cryptotis goodwini

Cryptotis goodwini.--Jackson, 27 April 1933, Proc. Biol. Soc. Washington 46:81; Goodwin, 12 December 1934, Bull. Amer. Mus. Nat. Hist. 68:6; Felten, 15 December 1958, Senckenbergiana Biologica 39:218; Hall and Kelson, 31 March 1959, The Mammals of North America 1:61; Genoways and Choate, 1 December 1967, Proc. Biol. Soc. Washington 80:204; Choate, 30 December 1970; Univ. Kansas Pub. Mus. Nat. Hist. 19:249; Hall, 3 April 1981, The Mammals of North America 1:60.

Cryptotis nigrescens.--Burt and Stirton, 22 September 1961, Univ. Michigan Mus. Zool. Misc. Pub. 117:21 (in part).

C[ryptotis]. goodwini.--Musser, 17 June 1964, Univ. Michigan Mus. Zool. Occas. Papers 636:7.

Holotype.--Skin and skull of adult male, USNM 77074; collected 13 January 1896 by E. W. Nelson (collector number 9073); from Guatemala, Quetzaltenango, Calel, 10,200 ft.

Distribution.--Contiguous highland regions above 1100 m in the Mexican State of Chiapas and Guatemala, and in a separate highland area in northern El Salvador. The

population in El Salvador probably extends northward along the Merendon Cordillera into western Honduras.

Description.--Size large for the genus (Table 5); tail short, averaging 29 mm, or ca. 35% of head and body length; front feet large and claws broadened; the dorsal guard hairs normally 6-8 mm long; dorsal pelage Saccardo's Umber/Prout's Brown/Mummy Brown; ventral pelage somewhat lighter than dorsum, Light Drab/Drab to almost Wood Brown; dorsal fur three-banded: basal 5/6ths of hairs silvery gray, followed by a thin, very pale brown band, grading into dark brown tip.

Rostrum of normal length (PL/CBL = 43.6% ± 0.7, n = 20) for the genus; usually (83%, n = 30) two well developed dorsal foramina; zygomatic plate not elongate (ZP/PL = 21.1%, n = 20), anterior border usually aligned with mesostyle-metastyle valley or metastyle of M1; posterior border of zygomatic plate aligned with posterior base of maxillary process; upper toothrow uncrowded, U4 aligned with toothrow and usually visible in labial view; P4, M1, M2 only very slightly recessed on posterior border; M3 normally with paracrista, paracone, precentrocrista, mesostyle, and very short postcentrocrista (all pigmented), and a well developed, pigmented protocone; hypocone on M3 is absent or poorly

developed; dentition not bulbous.

Mandible relatively long and of moderate breadth for the genus; coronoid process joins horizontal ramus at a relatively wide angle; distance between coronoid process and posterior border of m3 is long; viewed posteriorly, articular process generally moderately tall and wide, with a moderately broad lower articular facet; lower sigmoid notch deep; posterior border of lower incisor extends to posterior cingulum of p4; entoconid normally absent (86%, n = 29), but, if present, always poorly developed (14%).

Comparisons.--Cryptotis goodwini is the largest of the five species of shrews with enlarged forefeet and claws.

Cryptotis alticola.--Cryptotis goodwini differs in lack of a foramen posterior to the external capitular facet (0% vs. 58%); greater likelihood of having a foramen developed dorsal to the external capitular facet on one or both (95% vs. 52%) sides of the skull; relatively narrower palate; relatively shorter mandible.

Cryptotis goldmani.--Cryptotis goodwini has a relatively shorter tail; lacks a foramen posterior to the external capitular facet (0% vs. 95.5%); usually has a foramen developed dorsal to the external capitular facet on one or both (95% vs. 46%) sides of the skull; normally lacks

an entoconid on m3.

Remarks.--The known biology of C. goodwini previously was summarized by Choate (1970) and Choate and Fleharty (1974). Cryptotis goodwini has been found in high elevation forests of pine sometimes mixed with firs, oaks, and other species. Severe frosts are associated with at least some of their habitats (Goldman, 1951). Most specimens are from localities 1200 m or more in elevation, but Choate (1970:251) reports a specimen from Finca Xicacao as ca. 3000 ft. However, no elevation is given on the specimen tag for this specimen, and Xicacao is located in a region greater than 1000 m in elevation.

Specific reproductive data for C. goodwini are lacking. Our inspection of study skins of males from 4-15 January (n = 6), 5-22 May (2), 20 August (3), and 27 December (1) yielded none with well developed lateral glands.

Few specimens of C. alticola, C. goldmani, C. goodwini, or C. griseoventris have weights associated with them. Mean weight of seven adult male C. goodwini is 16.5 g (± 1.0, range = 15.7 - 18.7).

Cryptotis griseoventris

Cryptotis griseoventris.--Jackson, 27 April 1933, Proc.

Biol. Soc. Washington 46:80; Hall and Kelson, 31 March 1959, The Mammals of North America 1:60.

Cryptotis goldmani goldmani.--Choate, 30 December 1970; Univ. Kansas Pub. Mus. Nat. Hist. 19:247 (in part); Hall, 3 April 1981, The Mammals of North America 1:59 (in part).

Holotype.--Skin and skull of adult male, USNM 75894; collected 4 October 1895 by E. W. Nelson and E. A. Goldman (collector number 8545); from Mexico, Chiapas, San Cristóbal, 9500 ft.

Distribution.--Above at least 2000 m in conterminous highland areas of Guatemala and the Mexican State of Chiapas.

Description.--Size medium for the genus (Table 5); tail moderately long, averaging 29 mm, or ca. 38% of head and body length; front feet enlarged and claws broad; the dorsal guard hairs normally about 6-8 mm long; dorsal pelage Mummy Brown to Bister; ventral fur Light Drab to Drab, somewhat paler than dorsum; dorsal fur three-banded: basal 5/6ths of hairs silvery gray, followed by a thin, lightly colored band, grading into dark brown at the tip.

Rostrum of normal length (PL/CBL = 43.8% $\pm$ 0.8, n =

20) for the genus; usually (92%, n = 24) two well developed dorsal foramina; zygomatic plate not elongate (ZP/PL = 22.3%, n = 20), anterior border usually aligned with mesostyle-metastyle valley, metastyle of M1, or parastyle of M2; posterior border of zygomatic plate aligned with posterior base of maxillary process; upper toothrow uncrowded, U4 aligned with toothrow and partially visible in labial view; P4, M1, M2 only very slightly recessed on posterior border; M3 normally with paracrista, paracone, precentrocrista, mesostyle, and very short postcentrocrista (all pigmented), and a well developed, lightly pigmented protocone; hypocone on M3 is absent or extremely poorly developed; dentition not bulbous.

Mandible relatively long and of moderate breadth for the genus; coronoid process joins horizontal ramus at a relatively wide angle; distance between coronoid process and posterior border of m3 is long; viewed posteriorly, articular process tall and wide, with a broad lower articular facet and a relatively shallow lingual notch between articular facets; lower sigmoid notch deep; posterior border of lower incisor extends to posterior cingulum of p4; entoconid absent (100%, n = 23).

Comparisons.--*Cryptotis griseoventris* has a relatively

and absolutely longer molariform toothrow than any of the other four species.

Cryptotis alticola.--C. griseoventris has a relatively longer tail; lacks a foramen posterior to external capitular facet; is more likely to possess a foramen dorsal to posterior external capitular facet (96% vs. 52%) and two well developed dorsal foramina (92% vs. 57%); has a relatively and absolutely narrower palate; has a unicuspid toothrow that is relatively and absolutely longer; has a relatively shorter mandible.

Cryptotis goldmani.--C. griseoventris lacks a foramen posterior to external capitular facet; is more likely to possess a foramen dorsal to posterior external capitular facet (96% vs. 46%) and two well developed dorsal foramina (92% vs. 48%); has a unicuspid toothrow that is relatively and absolutely longer.

Cryptotis goodwini.--C. griseoventris is smaller and has a unicuspid toothrow that is relatively longer.

Remarks.--Specimens of C. griseoventris have been collected above at least 2100 m in mixed forests dominated by pines and firs and in oak-dominated cloud forest. Some areas inhabited by this small-eared shrew undergo nightly winter frosts and occasional snow

(Goldman, 1951).

No reproductive data are available for C. griseoventris. None of the skins we inspected of adult males collected 25-30 September (n = 4), 2-6 October (2), and 25-31 December (10) had obvious lateral glands.

Cryptotis "C", new species

Fig. 25

Holotype.--Skull of pregnant adult female with fluid-preserved body, KU 144611; collected 21 November 1991 by Peter Holm and Gustavo Cruz. Skull nearly complete, but with a hole in the dorsal braincase and lacking left tympanic; fluid-preserved body intact.

Type locality.--Honduras: Comayagua Department; Reserva Biológica Cordillera de Montecillos; 2.5 km N, 1.6 km E Cerro San Juanillo (14°30'N, 87°53'W; $^{16}03.4$ N, $^{4}05.7$ E), 1730 m. The holotype was found dead in mixed pine and broadleaf forest.

Distribution.--Known only from the type locality; probably occurs in high elevation (>1000 m) pine forest and mixed pine forest in highland areas contiguous with the Cordillera de Montecillos.

Measurements of Holotype.--Total length, 80; tail, 25; hind foot, 14; ear, 6; condylobasal length, 20.3;

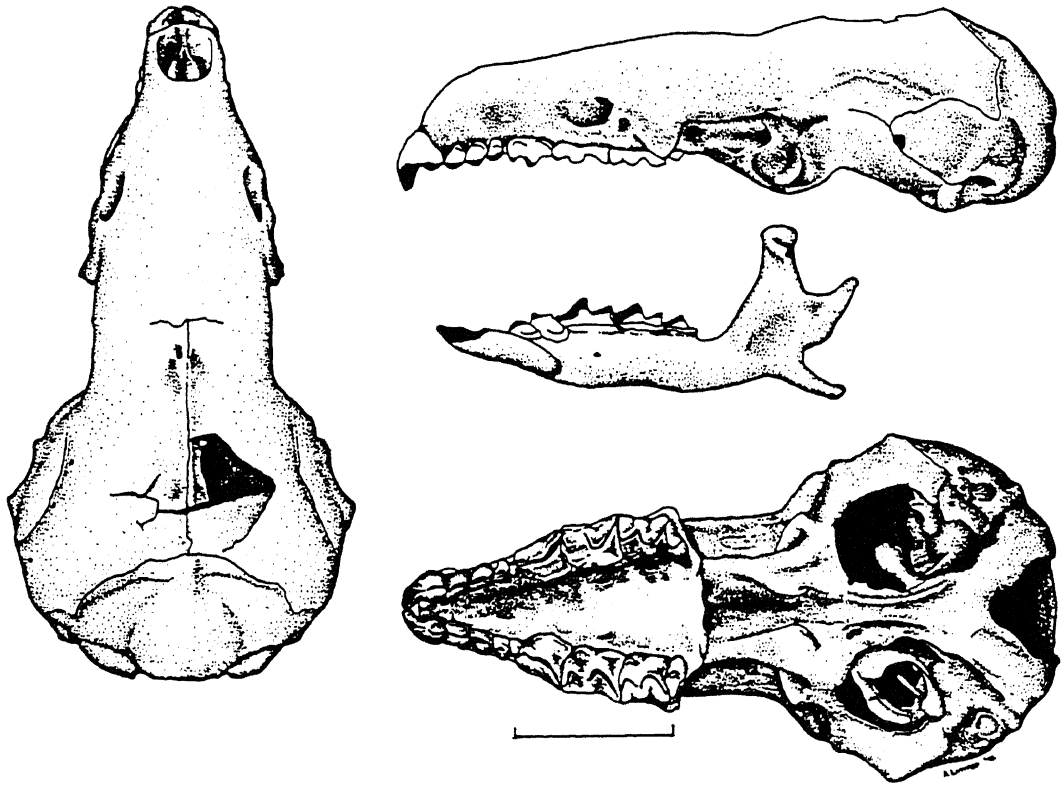

Figure 25. Dorsal and ventral views of the skull and lateral view of the skull and mandible of the holotype of Cryptotis "C" (KU 144611).

palatal length, 8.8; maxillary breadth, 6.4; interorbital breadth, 5.3; maxillary toothrow, 7.5; cranial breadth, 10.8; mandibular toothrow, 5.9 (see Tables 5 and 6). The external measurements were taken from the fluid-preserved body prior to removal of the skull.

Diagnosis.--A medium sized species of the genus Cryptotis characterized by its short tail, enlarged front feet and broad claws, zygomatic plate with posterior border aligned with the posterior border of the maxillary process, lack of a foramen posterior to the external capitulary facet, simple M3, wide angle between the coronoid process and the horizontal ramus of the mandible, and a tall, broad articular process.

Description.--Size medium for the genus (Table 5); tail short, 25 mm, or 31% of head and body length; front feet large and claws broad; dorsal guard hairs about 5-7 mm long; dorsal pelage of fluid-preserved holotype is Mummy Brown to Fuscous when air dried; venter is Brownish Olive and appears to be somewhat paler than dorsum; dorsal fur two-banded, basal 3/4ths silvery gray, distal 1/4 grading from pale brown to brown tip.

Rostrum of normal length (PL/CBL = 43.3%) for the genus; two well developed dorsal foramina; zygomatic plate long (ZP/PL = 25%), anterior border aligned with

metastyle of M1; posterior border of zygomatic plate slightly posterior to posterior base of maxillary process; upper toothrow uncrowded, U4 aligned with toothrow and partially visible in labial view; P4, M1, M2 only very slightly recessed on posterior border; M3 has paracrista, paracone, precentrocrista, mesostyle, and very short postcentrocrista, and a well developed protocone (because of wear, it is not certain whether protocone was pigmented); hypocone on M3 is absent or poorly developed; dentition not bulbous.

Mandible relatively long and of moderate breadth; coronoid process joins horizontal ramus at a relatively wide angle; distance between coronoid process and posterior border of m3 is long; viewed posteriorly, articular process tall and wide, with a broad lower articular facet and a relatively shallow lingual notch between articular facets; lower sigmoid notch deep; posterior border of lower incisor extends to posterior cingulum of p4; because of wear, it can not be determined whether an entoconid was present in talonid of m3.

Comparisons.--*Cryptotis* "C" has a longer zygomatic plate than the other four species of large-footed shrews.

Cryptotis alticola.--*Cryptotis* "C" lacks a foramen

posterior to external capitular facet and possesses a foramen dorsal to posterior external capitular facet; two well developed dorsal foramina; relatively and absolutely narrower palate.

Cryptotis goldmani.--Cryptotis "C" is larger overall and has a relatively and absolutely shorter tail; lacks a foramen posterior to external capitular facet and has a foramen dorsal to posterior external capitular facet; possesses two well developed dorsal foramina.

Cryptotis goodwini.--Cryptotis "C" is smaller in overall size and has a relatively and absolutely shorter tail.

Cryptotis griseoventris.--Cryptotis "C" has a relatively and absolutely shorter tail; relatively and absolutely shorter unicuspid toothrow.

Remarks.--The type and only known specimen of Cryptotis "C" is an adult female that was pregnant when captured on 21 November. She carried four embryos, three in the right horn of the uterus and one in the left (crown to rump length = 8 mm). This is the first record of a pregnancy in any of the large-footed shrews.

Key to the large-footed shrews

1. Foramen normally located posterior to the external

capitularfacet (Fig. 24B); foramen normally lacking dorsal to external capitular facet 2

2. Tail short (23-30 mm, ca. 33% of head and body length); foramen posterior to external capitular facet minute if present ..... C. alticola

2'. Tail long (24-36 mm, ca. 38% of head and body length); foramen posterior to external capitular facet large, usually present ..... C. goldmani

1'. Foramen normally posterior to the external capitular facet lacking (Fig. 24A); foramen usually present dorsal to external capitular facet 3

3. Unicuspid toothrow relatively long (2.5-2.9 mm, ca. 13.7% of CBL) .....C. griseoventris

3'. Unicuspid row not elongate (ca. 11.8 - 13% of CBL) 4

4. Size large (CBL = 20.0-22.8; HB = 75-94); zygomatic plate not elongate (ca. 9.2% of CBL) ... C. goodwini

4'. Size medium (CBL = 20.3; HB = 80); zygomatic plate elongate (10.8% of CBL) ..... Cryptotis "C"

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Specimens Examined

Cryptotis alticola (34).--MEXICO: COLIMA: Volcán de Fuego [= Volcán de Colima], 8800 ft (1 LACM). DISTRITO FEDERAL: Cerro Santa Rosa, Municipio Contreras, 3200 m (1 IBUNAM); Santa Rosa, 3000 m (1 UMMZ); Canyon [Cañon]

Contreras, 10,200 ft (1 UMMZ). JALISCO: 20 mi SE Autlán [de Navarro], 9000 ft (3 KU); 12 mi SW Ciudad Guzmán, 10,000 ft (3 KU); Volcán de Fuego [= Volcán de Colima], 9800 ft (1 KU - type of C. euryrhynchis). MEXICO: 45 km ESE Mexico City, Monte Río Frio (1 TCWC); N edge Refugio San Cayetano, 3 mi S Bosenchere, 8200 ft (1 UMMZ); 15.5 km S, 7 km E Zinacantepec [= San Miguel Zinacantepec], 3470 m (1 ENCB); Salazár, 8800-10,000 ft (3 USNM); Lagunas de Zempoala [10 mi NNW Cuernavaca - Choate, 1970] 9100 ft (3 USNM); 12 km ESE Amecameca, 11,500 ft (1 KU); N slope Volcán Toluca [= Nevado de Toluca; above San Juan de las Huertas], 11,500 ft (1 USNM); Mount Popocatepetl [Volcán de Popocatépetl], 11,500-13,500 ft (4 USNM). MICHOACAN: Sierra Patamba [Cerro Patamban], 9000 ft (1 KU); ca. 12 mi W Ciudad Hidalgo, 9150 ft (1 KU); 17.5 km NW Ciudad Hidalgo, 2980 m (1 ENCB). PUEBLA: Municipio San Martín Texmelucan, 10 km W San Juan Tetla, 3300-3400 m (5 IBUNAM).

Additional records (from Choate, 1970:246, unless otherwise noted).--MEXICO: JALISCO: N slope Nevado de Colima [= Volcán de Colima], 8000-10,000 ft. MEXICO: Cerro Ajusco, 11,000 ft; Monte Río Frio, 45 km ESE Mexico City, 10,500 ft (Davis, 1944). MICHOACAN: Cerro de Tancítaro [= Pico de Tancítaro], 9000-12,000 ft.

Cryptotis goldmani (43).--MEXICO: GUERRERO: Municipio Atoyac de Alvarez, Los Retrocesos 1550 m (2 MZFC); Municipio Tlacotepec [Mpio. General Heliodoro Castillo], El Iris (2 MZFC); 3 mi NW Omiltemi, 2300 m (1 USNM); 2 mi W Omiltemi, 7800-7900 ft (4 TCWC); Omiltemi, 5700-8700 ft, 2450 m (1 IBUNAM, 3 KU, 6 LACM, 3 MZFC, 5 USNM); mountains near [N and NW of] Chilpancingo, 9500-9800 ft (3 USNM); 7 mi SW Filo de Caballo, 8200 ft (2 TCWC). OAXACA: 2 km NE San Andres Chichuaxtla (1 UMMZ); km 158, Puerto Angel Road, lumber camp, 8375 ft (1 CAS); Ixtlan District, Comaltepec, Vista Hermosa (1 KU); Campamento Río Molino, 2300 m (2 KU); Santa María Ozolotepec [mountains near La Cieneguilla], 10,000 ft (6 USNM); Cerro Zempoaltepec, 8000-10,500 ft (3 USNM).

Additional records (from Choate, 1970:249).--MEXICO: GUERRERO: S slope Cerro Teotepec; 3 mi W Omiltemi, 8200 ft. OAXACA: Lachao; San Miguel Suchixtepec; 3 km SW San Miguel Suchixtepec; San Juan Ozolotepec; Mixteguilla; "near the City of Tehuantepec".

C. goodwini (35).--EL SALVADOR: SANTA ANA: Hacienda Montecristo. (1 SMF). GUATEMALA: BAJA VERAPAZ: 5 mi N, 1 mi W El Chol, 6000 ft (1 KU). CHIMALTENANGO: Santa Elena, 9900-10,000 ft (4 FMNH). HUEHUETENANGO: 3.5 mi SW San Juan Ixcoy, 10,120 ft (1 KU); San Mateo Ixtatlan

[San Mateo Ixtatán], ca. 4 km NW Santa Eulalia, Yayquich, 2950 m (1 UMMZ); Hacienda Chancol, 9500-11,000 ft (1 USNM). JALAPA: Mataquescuintla, 8400 ft (1 USNM). QUEZALTENANGO: Calel, 10,200 ft (13 USNM); Volcán Santa María, 9000-11,000 ft (2 USNM). SAN MARCOS: S slope Volcán Tajamulco, 10,000 ft (1 UMMZ). TOTONICAPAN: Cumbre María Tucum, 3000 m (8 UMMZ). MEXICO: CHIAPAS: Municipio Jaltenango, 17 km SE Finca Prusia; Reserva Ecológica El Triunfo, 2000 m (1 IBUNAM).

Additional records (from Choate [1970:251] unless otherwise indicated).--GUATEMALA: ALTA VERAPAZ: Xicacao. CHIMALTENANGO: Tecpam [=Tecpán], 9700 ft (Goodwin, 1934). SAN MARCOS: Finca La Paz, 1200 m.

C. griseoventris (27).--MEXICO: CHIAPAS: San Cristóbal [de] las Casas, 8000-9500 ft (8 USNM); 6 mi SE San Cristóbal [de] las Casas (1 MCZ). GUATEMALA: HUEHUETENANGO: Todos Santos Cuchumatán, 10,000 ft (18 USNM).

Cryptotis "C" (1).--HONDURAS: COMAYAGUA: Reserva Biológica Cordillera de Montecillos; 2.5 km N, 1.6 km E Cerro San Juanillo, 1730 m (1 KU - holotype).

C. mexicana mexicana (57).--MEXICO: CHIAPAS: 3 mi E Pueblo Nuevo Solistahuacan, 7000 ft (1 KU); OAXACA: 21.8

km (by road) S Vista Hermosa, 2100 m (1 KU); 31.6 km (by road) S Vista Hermosa, N slope Cerro Pelón, 2650 m (2 KU); NE slope Cerro Pelón, 2620 m (1 KU); Cerro San Felipe, 6 km W La Cumbre, 2670 m (2 KU); 2 km W La Cumbre, 2900 m (1 KU); 7 mi N Ixlan de Juarez, 10,000 ft (2 CAS); Llano de las Flores, 2800-2900 m (7 KU); 0.4 mi S Llano de las Flores, 9200 ft (1 TCWC); 11 mi NE (Tuxtepec road) Llano de las Flores, 9100 ft (1 UMMZ); 27.5 km NNE (by road) Llano de las Flores (8 LACM). PUEBLA: Vista Hermosa, 1500 m (1 KU); 7.5 mi NE Tezuitlan (1 MMNH); 5 mi NE Tezuitlan (2 MMNH); Distrito Ixtlán, 16 mi WSW La Esperanza (1 TCWC). VERACRUZ: Las Vigas, 8500 ft (21 KU); 11 km W Las Vigas, 8500 ft (1 KU); 5 mi E Las Vigas (1 TCWC); 4 km W Tlapacoyan, 1700 ft (3 KU).

C. mexicana nelsoni (4).--MEXICO: VERACRUZ: Volcán de Tuxtla [Volcán San Martín], 4800 ft (3 USNM; 1 MCZ).

C. mexicana obscura (33).--MEXICO: HIDALGO: Lago Tejocotal, 11 km E Acaxochitlan, 2250 m (2 KU); QUERETARO: 1 km S Ahuacatlán, Municipio Pinal de Amoles (1 MZFC); 1 km S Pinal de Amoles, Municipio Pinal de Amoles (11 MZFC); Pinal de Amoles, Municipio Pinal de Amoles, 2250-2460 m (8 ENCB). TAMAULIPAS: Rancho del Cielo, 5 mi NW Gomez Farias, 3500 ft (1 AMNH, 8 MMNH).

VERACRUZ: Zacualpan, 6000 ft (2 KU).

C. mexicana peregrina (20).--MEXICO: OAXACA: Río Molino, Puerto Angel road, km 153, 2250-2300 m (1 CAS, 1 KU, 2 UNAM); lumber camp, Puerto Angel road, km 158, 8375 ft (1 CAS); Río Jalatengo, Puerto Angel road, km 178, 4275 ft (4 CAS, 1 UNAM); Puerto Angel road, km 195, 3475 ft (1 UNAM); La Cima, Puerto Escondido road, km 184.5, 5750 ft (1 CAS); Puerto Escondido road, km 193, 4200 ft (1 CAS); Río Guajalote, 2000 m (2 KU); Sinai, 10 km E Nopala, 7200 ft (1 CAS); 20 mi S, 5 mi E Sola de Vega, 4800 ft (2 KU); 16 km SW Suchixtepec, 2000 m (2 ENCB).

INTRASPECIFIC AND INTERSPECIFIC VARIATION IN THE *CRYPTOTIS NIGRESCENS* SPECIES COMPLEX OF SMALL-EARED SHREWS (INSECTIVORA: SORICIDAE), WITH THE DESCRIPTION OF A NEW SPECIES FROM COLOMBIA

Small-eared shrews of the genus *Cryptotis* have a wide distribution, occurring in parts of North America, Central America, and northwestern South America. The genus reaches its greatest diversity in Mexico and Central America. Hall and Kelson (1959) recorded 25 species of *Cryptotis* in this region. In his revision of the Middle American *Cryptotis*, Choate (1970) recognized eight species of small-eared shrews in Mexico and Central America, and his taxonomy has been followed by most subsequent authors, including Hall (1981), Honacki et al. (1982), and Corbet and Hill (1991). More recently, we (Woodman and Timm, 1992, submitted, manuscript) recognized seven additional species from Costa Rica, Guatemala, Honduras, and Mexico, bringing the total to 15 species.

One poorly understood Central American group of *Cryptotis* is the *Cryptotis nigrescens* complex, which was known to occur from Guerrero, Mexico, through Central America to the Panama/Colombia border. Most species of small-eared shrews which occur from central Mexico

through northern South America are high elevation forms, inhabiting regions over 500 m. The C. nigrescens complex, which includes both high elevation and very low elevation taxa, is an exception. Choate (1970) provided the only recent comprehensive treatment of the taxonomy and distribution of C. nigrescens. He recognized one widely distributed species, C. nigrescens, which included three subspecies: Cryptotis nigrescens mayensis, occurring in the Yucatan Peninsula and known from one locality in Guerrero, Mexico; C. n. merriami, distributed from Chiapas, Mexico, to Honduras and El Salvador, and C. n. nigrescens, inhabiting Costa Rica and Panama to the Panama/Colombia border.

In his review of the Cryptotis of Middle America, Choate (1970) had few complete specimens of C. nigrescens upon which to base his study of the species. Of the 237 C. n. mayensis available at that time, all but 10 were mandibles and partial crania from owl pellets, cave deposits, or Mayan ruins. Similarly, 15 of the 25 specimens available for C. n. merriami were from owl pellets, and only 29 specimens of C. n. nigrescens were available for study. Recent collecting in Mexico has added important new specimens of C. n. mayensis and C. n. merriami, and work in Panama and Costa Rica has tremendously increased the number of C.

n. nigrescens in museum collections. This wealth of new material led us to review this complex more thoroughly than was possible previously.

Cryptotis nigrescens was considered to be distinguished by its short rostrum; bulbous dentition; equal development of anterior and posterior portions of M1; unrecessed posterior margins of P4, M1, and M2; simple M3; and lack of an entoconid in m3 (Choate, 1970). However, there is much variation within this taxon, and the polarizations of these characters have not been defined.

Systematics of the genus Cryptotis are not resolved as yet and will be addressed at a later date. In this paper, species previously called C. nigrescens are referred to informally as members of the "C. nigrescens group".

The purposes of this paper are to: 1) redescribe and illustrate four previously described species in the C. nigrescens group; 2) describe and illustrate a species new to science; 3) map the geographic distributions of these species; and 4) review the available information on reproduction, elevational distribution, and habitat for the members of this complex.

Methods

Cranial and mandibular measurements were taken to the nearest 0.1 mm using either an ocular micrometer in a binocular microscope or a hand-held dial caliper. Skin measurements are those recorded by the collector, except for head and body length, which we calculated by subtracting the recorded tail length from the total length. All measurements are in millimeters. Dental terminology follows Choate (1970). Measurements used in our analyses follow Woodman and Timm (submitted). These include head and body length (HB); tail length (TL); condylobasal length (CBL); cranial breadth (CB); breadth of zygomatic plate (ZP); postorbital breadth (PO); breadth of palate across first unicuspids (U1B); breadth of palate across third unicuspids (U3B); breadth of palate across second molars (M2B); palatal length (PL); upper toothrow length (TR); unicuspid toothrow length (UTR); molariform toothrow (MTR); posterior width of M1 (WM1); mandibular length, from inferior sigmoid notch to mental foramen (ML); height of coronoid process (HCP); height of coronoid valley (HCV); height of articular condyle (HAC); breadth of articular condyle (BAC); articular condyle to posterior edge of m3 (AC3); lower toothrow length (TRD); lower molariform toothrow (LMT); length of m1 (m1L). Unless otherwise stated univariate

statistics are mean ± standard deviation. All capitalized color names follow Ridgeway (1912). Localities and elevations are taken directly from specimen tags and represent the descriptions of the original collectors. We provide corrections and additions in brackets. We do not convert distances measured in miles or elevations measured in feet to the metric system to avoid inferring a level of accuracy greater than that originally recorded by the collector. Specimens from archeological or paleontological contexts are not used in statistical analyses or plotted on maps because of the possibility of temporal variation in size, shape, or range. Number of specimens from archeological or paleontological sites is calculated as the minimum number of individuals.

Analyses of variance (anova), correlation matrices, and multivariate analyses were carried out using BMDP on the University of Kansas Academic Computing Services' IBM VM/CMS computer system. Regression statistics were calculated using MINITAB (Release 8, 1991).

Male and female Cryptotis are difficult to tell apart, and few tests for sexual dimorphism within the genus have been carried out, at least partly because there were few good series of sexed individuals. We tested for sexual variation in C. nigrescens using our

two largest series of sexed individuals: one was a series of 16 skins and 13 skulls of males and 16 skins and 12 skulls of females from Monteverde, Costa Rica; the second consisted of 9 skins and 13 skulls of males and 8 skins and 10 skulls of females from near San Félix (including Cerro Bollo), Panama. A correlation matrix was calculated for 2 skin (HB, TL) and 18 cranio-mandibular variables (CBL, CB, ZP, PO, U1B, U3B, M2B, PL, TR, UTR, MTR, LM, HCP, HAP, BAC, TRD, AC3, HAV). Variables then were culled so that no two variables in the remaining data set had a correlation coefficient of 0.75 or greater. A two-way anova was calculated for each of the remaining 9 variables (HB, TL, CBL, ZP, UTR, MTR, HAP, BAC, HAV). Both sex and locality (Monteverde vs. San Félix) were tested as sources of variance to separate effects of sexual dimorphism and geographic variation. Statistical significance was determined using a Brown-Forsythe test for equality of means, which does not assume equality of the variances. Protected alpha values were not used despite a lack of independence among the variables tested, because protected values would have increased the likelihood of making Type II errors (i.e., incorrectly accepting no difference between males and females or between localities). We subsequently attempted to separate

males and females using discriminant function analysis (DFA) on the 18 skull and mandible measurements; for this test, specimens from Monteverde and San Félix were run separately. A protected F-to-enter (alpha = 0.05/10 comparisons = 0.005) was used for DFA because of the multiple variables being considered. A more protected F-to-enter (alpha = 0.05/19 comparisons = 0.0026) was not used beause of the increased likelihood of making a Type II error.

Although the probability that there was a difference between males and females was < 0.30 for six of nine variables (see Results, below), the actual differences between means of males and females was slight, often below our ability to measure. Because sexual variation did not inhibit our ability to detect geographic variation within a species, we used males, females, and unsexed individuals in all subsequent analyses.

Elevational and geographic distributions and the correlation of character states to these distributions were examined for all members of the C. nigrescens group.

Crania and mandibles of Cryptotis derived from owl pellets and identified previously as C. n. mayensis were reported from the Mexican State of Guerrero by Choate (1970; see Species Accounts, below). Because these

specimens were from far outside the range of all other populations on the Yucatan Peninsula, and because of the geographical barriers and habitat differences between the two areas, we considered that specimens from Guerrero might prove to be either misidentified or an undescribed species. The fragmentary nature of the specimens from Guerrero did not yield characters useful for separating them from populations on the Yucatan Peninsula and limited the measurements that could be taken from them. We carried out DFAs and PCAs in order to test the overall similarity of the two groups of specimens. Crania and mandibles were tested separately, because these elements are disassociated in all known specimens from Guerrero. Analyses of crania included six variables (ZP, PO, M2B, PL, MTR, WM1) measured on 21 C. n. mayensis from the Yucatan Peninsula, 15 C. n. merriami, and 20 specimens from Guerrero; analyses carried out on mandibles contained eight variables (LM, HCP, HAV, HAP, BAC, TRD, m1L, AC3) from 21 C. n. mayensis, 23 C. n. merriami, and seven mandibles from Guerrero. Specimens of C. n. merriami were included to determine if these measurements were useful for distinguishing groups. Regressions of factor 1 vs. factor 3 scores from the PCA of cranial measurements were calculated individually for each group to determine

if within group trends could be detected. Because PCA treats all individuals as though they were from a single population, we hypothesized that any trends (or the lack of trends) indicated by the regressions should be similar for all three groups.

Because of possible geographic variation, and because of their fragmentary nature, specimens from Guerrero were not included with other C. n. mayensis in calculations of univariate statistics or in other tests involving this taxon.

The following acronyms are use for institutions in which specimens are deposited: American Museum of Natural History, New York (AMNH); Angelo State University Natural History Collections, San Angelo (ASNHC); Escuela Nacional de Ciencias Biológicas, Mexico (ENCB); Field Museum of Natural History, Chicago (FMNH); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico (IBUNAM); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia (INBio); University of Kansas Museum of Natural History, Lawrence (KU); Los Angeles County Museum, Los Angeles (LACM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of the High Plains, Fort Hays State University, Hays (MHP); James Ford Bell Museum of Natural History, University of Minnesota, Minneapolis

(MMNH); Museo Nacional de Costa Rica, San José (MNCR); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Royal Ontario Museum, Toronto (ROM); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Universidad Nacional Autónoma de Honduras, Tegucigalpa (UNAH); U.S. National Museum, Washington, D.C. (USNM).

Results

Two-way anovas used to test for sexual variation in specimens from Monteverde and San Félix revealed two variables that showed a statistically significant difference between males and females: UTR ($P = 0.0081$) and HAV ($P = 0.0366$). In addition, CBL ($P = 0.0689$) was close to being significantly different, and three variables (HB, TL, HAP) had probabilities < 0.30 of being distinct. In all four cranial and mandibular variables (UTR, HAV, CBL, HAP), females averaged slightly larger than males. Males and females from Monteverde showed a slightly greater degree of differentiation than specimens from San Félix. However, actual differences between male and female means in both groups was small, ranging from 0.06 to 0.10 mm among the variables showing statistical significance. Males from both localities averaged larger than females in HB, and males from San Félix averaged larger than females in TL;

females from Monteverde had a larger TL. In contrast to the sex term, five of seven cranio-mandibular variables and both skin variables showed very highly significant ($\underline{P}$ = 0.0001 to 0.0000) variation between localities. Of the remaining two variables, MTR was significantly different ($\underline{P}$ = 0.0153) between localities, and ZP showed no statistical difference ($\underline{P}$ = 0.4041) between localities. For all variables except ZP, specimens from San Félix averaged larger than those from Monteverde. In fact, in all cases (except ZP) males from San Félix averaged larger than females from Monteverde. The interaction between sex and locality was significant for only TL ($\underline{P}$ = 0.0469).

Only two variables (TR, MTR) entered into the discriminant model of the DFA used to test for variation between males and females from Monteverde. No other variables showed sufficient intersexual variation in combination with TR and MTR to be significant. The two-variable model was able to classify only 68% of specimens correctly using a jackknifed classification; four males and four females were incorrectly identified. Males and females from San Félix showed insufficient differences to enter any variables into the DFA.

Analyses of crania and mandibles of $\underline{C}$. $\underline{n}$. $\underline{mayensis}$ failed to indicate any variables which were useful in

distinguishing between specimens from the Yucatan Peninsula and those from Guerrero. DFA of crania entered only a single variable (M1W) into the analysis, which correctly identified only 52% of specimens using a jackknifed classification. The DFA of mandibles utilized two variables (ML, HCP), which correctly classified 91% of C. n. merriami, but only 71% of specimens from Guerrero and fewer than half of those from the Yucatan (Fig. 26). Intermixing between the two described taxa was minimal; only two C. n. merriami and two C. n. mayensis from the Yucatan were incorrectly identified as the other taxon. Most misclassifications occurred between specimens from Guerrero and the Yucatan Peninsula. A plot of the specimens on factor axes 1 and 3 from the PCA of crania indicates great overlap between C. n. mayensis from the two areas (Fig. 27). All variables except ZP loaded out heavily on factor 1, providing a measure of overall size of the specimens. Factor 3 is a shape axis, providing a contrast between PL and a negatively weighted M2B. (Factor 2 from this analysis represented a contrast between a heavily weighted ZP and a slightly negatively weighted M1W; it did not aid in separating any groups.) In this plot, C. n. mayensis and C. n. merriami are separated by a combination of size and shape. Cryptotis nigrescens

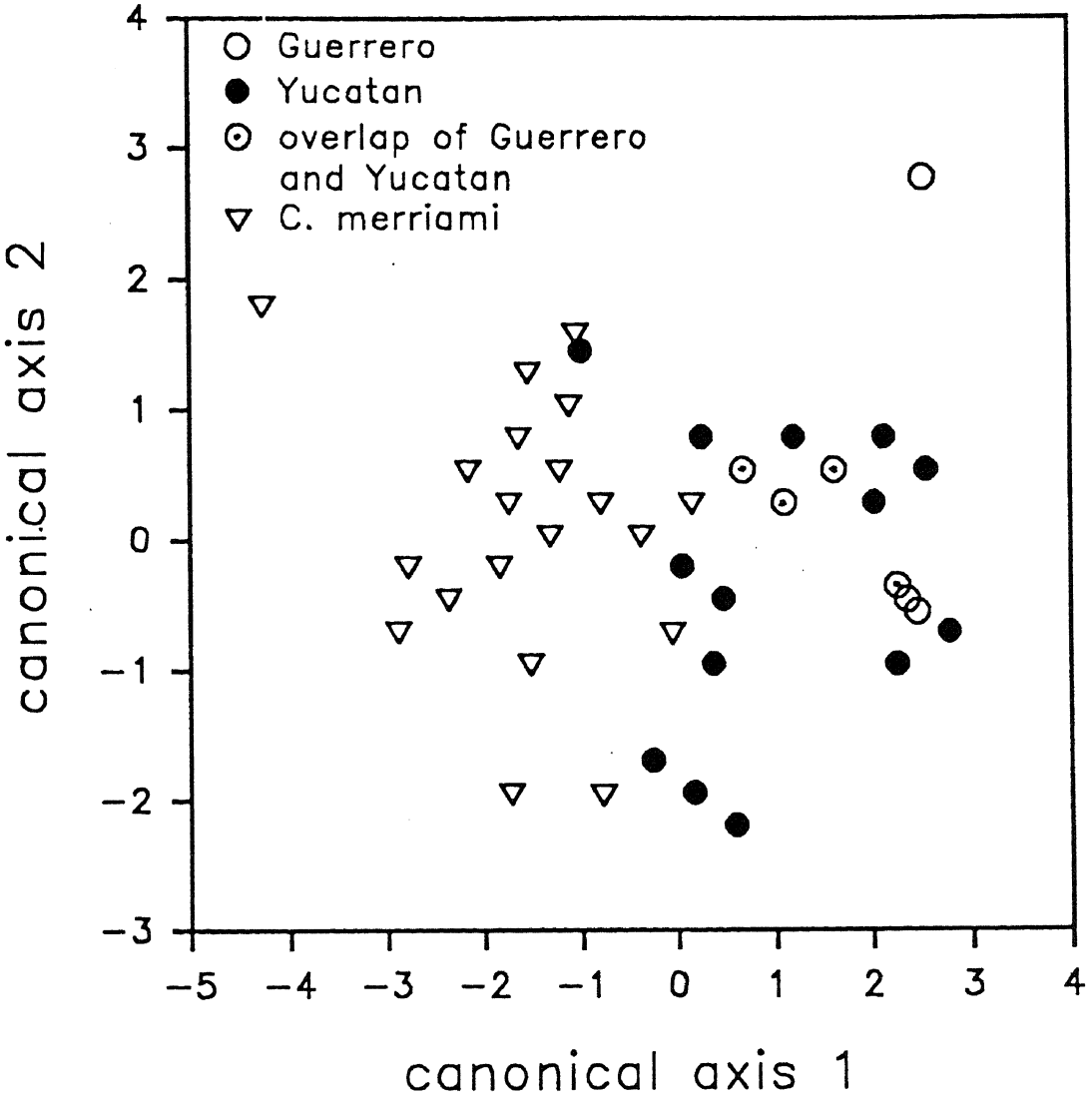

Fig. 26. Plot of specimens of C. mayensis from Guerrero and the Yucatan Peninsula and C. merriami on canonical axes 1 and 2 from a DFA of mandibular variables.

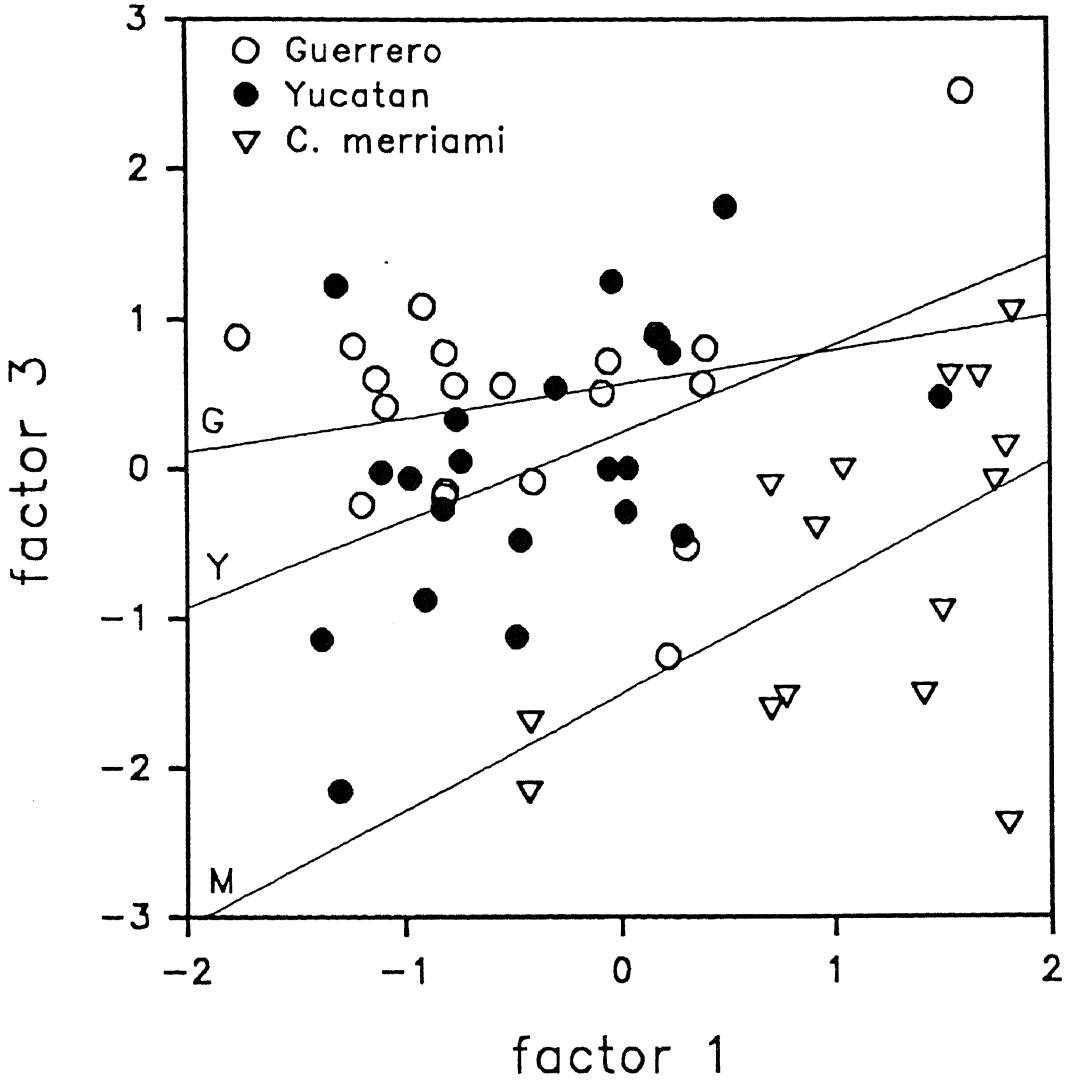

Fig. 27. Plot of specimens of C. mayensis from Guerrero and the Yucatan Peninsula and C. merriami on factor axes 1 and 3 from a PCA of cranial variables.

merriami tends to be larger cranially than C. n. mayensis, and, at any given size, C. n. mayensis has a longer but narrower palate than C. n. merriami. Regressions calculated for each of the groups shows both C. n. merriami ($P = 0.040$, $R = 28.5\%$) and C. n. mayensis from the Yucatan ($P = 0.034$, $R = 21.5\%$) tend to have narrower palates as size increases. In contrast, specimens from Guerrero do not show this trend ($P = 0.313$, $R = 5.6\%$); palatal shape remains within a relatively narrow range regardless of size. In the plot of specimens on factor 1 and factor 2 from the PCA of mandibles (Fig. 28), specimens of from the Yucatan Peninsula and Guerrero again are intermixed. Factor 1 in this analysis is a size axis incorporating all variables except m1L, and factor 2 is a contrast between a combination of m1L, LMT, and LM and a negatively weighted HCP. In contrast to the PCA of crania, C. n. merriami and C. n. mayensis do not separate out on the basis of size. Instead, the two separate out on factor 2; C. n. mayensis has a relatively shorter mandible and toothrow (m1L, LMT, LM) and a taller coronoid process than C. n. merriami.

Discussion

The few studies that have investigated sexual dimorphism in Cryptotis indicate that sexual differences

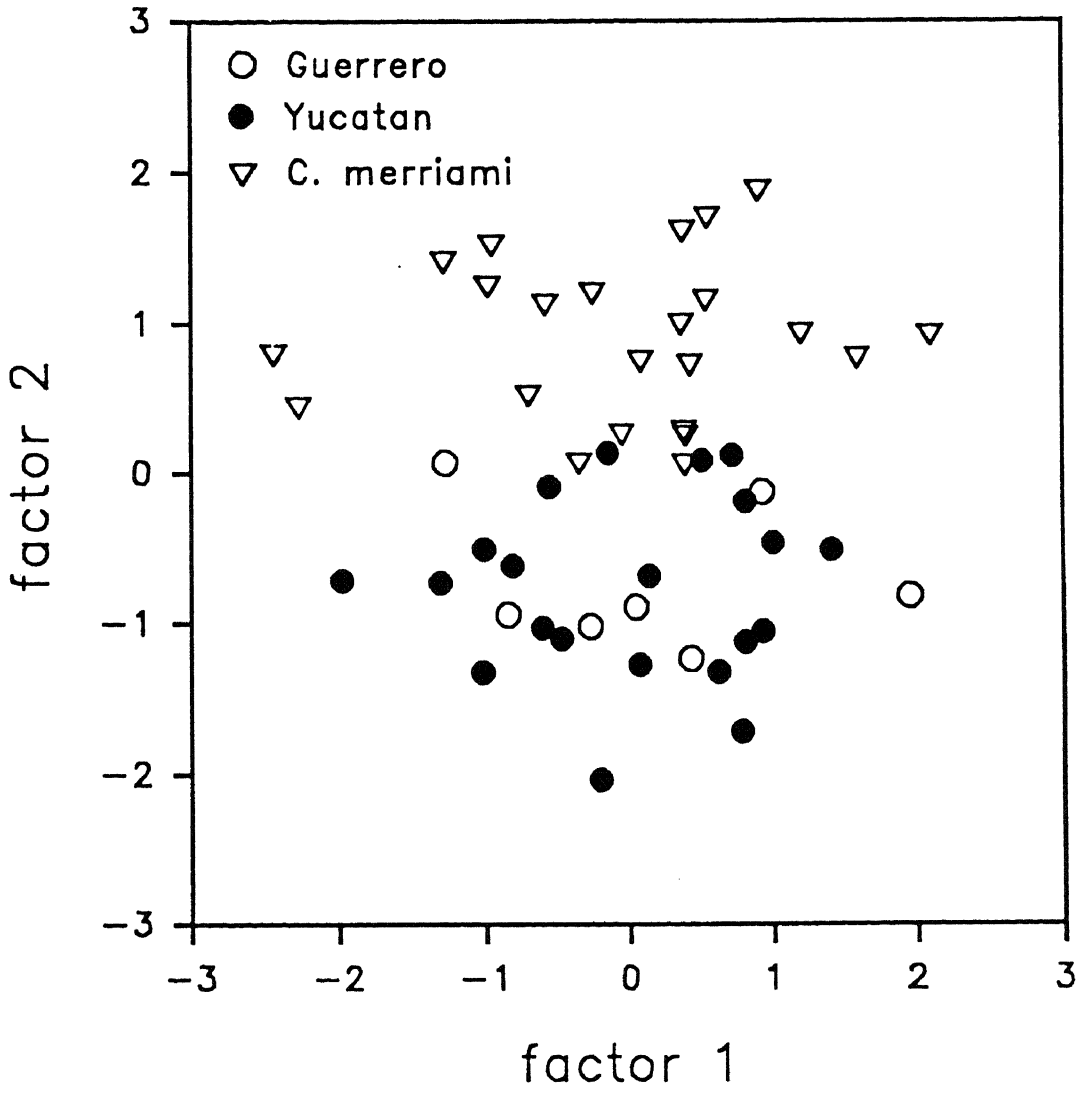

Fig. 28. Plot of specimens of C. mayensis from Guerrero and the Yucatan Peninsula and C. merriami on factor axes 1 and 2 from a PCA of mandibular variables.

in mensural variables are minor at most. Choate (1970) found length of maxillary toothrow was the only measurement that was significantly different between the sexes in his morphometric examination of C. mexicana from near Jalapa, Veracruz, Mexico. We (Woodman and Timm, submitted) found only one of 19 variables to differ significantly between males and females of C. gracilis in Costa Rica and Panama; zygomatic plate length was significantly longer in females.

Our analysis of sexual variation in C. nigrescens suggests minor levels of sexual dimorphism with females slightly larger than males. However, the overlap between males and females for each measurement is great, and, more importantly, differences between the sexes are considerably less than differences between geographic localities. The biological significance, if any, of these sexual differences is unknown, and they do not influence statistical tests among populations or contribute significantly to overall patterns of geographic variation.

My study of geographical distribution and morphological variation in the C. nigrescens complex indicates the presence of five morphological taxa which correspond to five geographical regions. Based on our investigations, we recognize four previously described

species: C. mayensis occurs in the Yucatan Peninsula and is known from an isolated locality in Guerrero; C. merriami has a patchy distribution at higher elevations from Chiapas, Mexico, to northern Costa Rica; C. nigrescens inhabits conterminous highlands in Costa Rica and Panama; and C. mera is known from two isolated mountaintops along the Panama/Colombia border. In addition we describe a new species from the Central Cordillera of Colombia. This last taxon extends the known distribution of the C. nigrescens complex southward into northern Colombia.

Within the C. nigrescens complex, there appears to be a fundamental morphological division between the Mexican and northern Central American taxa (C. mayensis and C. merriami) and the three species from southern Central American and Colombia. The two northern species appear to be more derived and more closely related to each other than either is to any of the southern species. Both C. mayensis and C. merriami typically have a well-developed posterior branch of the sinus canal posterior to the dorsal articular facet (external capitular facet of McDowell, 1958), no foramen dorsal to the dorsal articular facet, only a single dorsal foramen located on either the left or right frontal, and a relatively long zygomatic plate. Relationships among the southern

species are unclear at this time. The two subgroups meet or come close to meeting, in the Tilarán Highlands of northern Costa Rica, from which we have identified both C. merriami and C. nigrescens (sensu strictu). The story becomes all the more complex, because the Costa Rican C. merriami is a disjunct population far removed from the main range of C. merriami, which extends as far south as northern Nicaragua, and further study of this population may show that it represents a distinct species. It appears that the lowlands of southern Nicaragua have had a fundamental role in the isolation and subsequent morphological evolution of the members of the C. nigrescens group, first in separating northern taxa from southern taxa, and now in separating the Costa Rican population of C. merriami from the main range of C. merriami farther north. Study of the relationships among members of the C. nigrescens group is a subject of our continuing research.

Species Accounts

In the following accounts, species are arranged geographically, roughly from north to south.

Cryptotis mayensis (Merriam, 1901)

Fig. 29

Blarina mayensis C. H. Merriam, 29 November 1901, Proc.

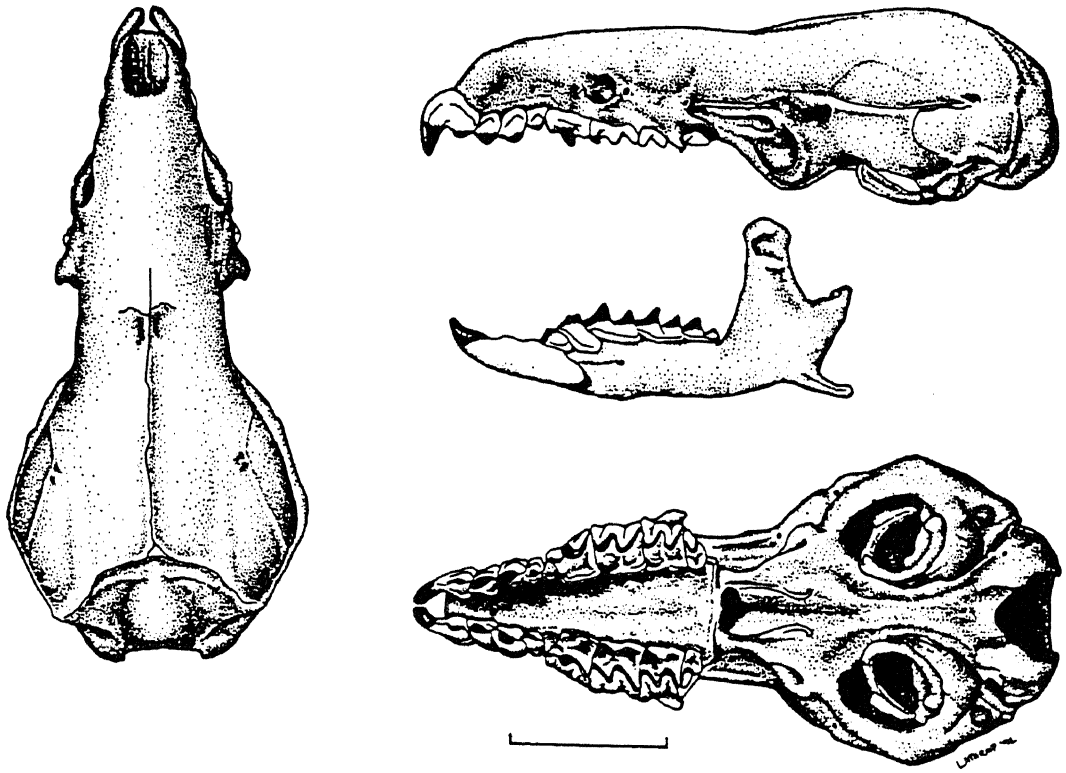

Fig. 29. Dorsal, ventral, and lateral views of the skull and lateral view of the skull and mandible of C. mayensis (ASNHC 6071).

Washington Acad. Sci. 3:559.

Cryptotis mayensis G. S. Miller, Jr., 31 December 1912, Bull. U.S. Natl. Mus. 79:26; R. T. Hatt, 18 August 1938, J. Mamm. 19:334; P. Hershkovitz, 10 July 1951, Fieldiana-Zool. 31:522; R. T. Hatt et al., March 1953, Cranbrook Inst. Sci. Bull. 33:59; E. R. Hall and K. R. Kelson, 31 March 1959, The mammals of North America 1:61; T. Alvarez and A. Martinez G., 4 August 1967, Southwest. Nat. 12:205; R. L. Peterson, 26 November 1968, J. Mamm. 49:796.

Blarina mexicana G. F. Gaumer, 1917, Monografía de los mamíferos de Yucatán, p. 249 (part).

Cryptotis micrura A. Murie, 15 July 1935, Misc. Publ. Mus. Zool., Univ. Michigan 26:17 (part); E. R. Hall and K. R. Kelson, 31 March 1959, The mammals of North America 1:62 (part).

Cryptotis nigrescens mayensis J. R. Choate, 30 December 1970, Univ. Kansas Pubs. Mus. Nat. Hist. 19:275; E. R. Hall, 3 April 1981, The mammals of North America 1:63; R. C. Dowler and M. D. Engstrom, 15 December 1988, Ann. Carnegie Mus. 57:160.

Holotype.--Skin and skull of subadult female, U.S.

National Museum of Natural History no. 108087, obtained by E. W. Nelson and E. A. Goldman (collector number 14495) 5 February 1901 from Mexico, Yucatán, Chichén Itzá.

Distribution.--Known primarily from below 100 m on the Yucatan Peninsula of Mexico and adjacent Belize and Guatemala (Fig. 30). Also known from remains isolated from owl pellets collected in a cave at 650 m, in the Cañon del Zopilote, Guerrero, Mexico.

Description.--A medium size Cryptotis, HB averaging 70 (Table 7); tail short, averaging 41% (± 2%, n = 10) of head and body length; dorsal hairs about 3 mm long, ranging from about 2 to 4 mm, three-banded; dorsum often has mottled, salt and pepper appearance; dorsal pelage variable: Pale Ecru-Drab and Drab, Light Drab, Light Mouse Gray to Deep Mouse Gray, Pale Mouse Gray or Mouse Gray with touches of Olive Brown; lateral pelage from Smoke Gray to Mouse Gray; venter slightly lighter than dorsum, may include one or more of the following: Pale Olive Gray, Light Olive Gray, Light Grayish Olive, Pale Mouse Gray to Light Mouse Gray.

Rostrum narrow and of normal length (PL/CBL = 43.4 ± 1.2, n = 10); interorbital area moderately wide; usually only one dorsal foramen (81%, n = 65) located on either

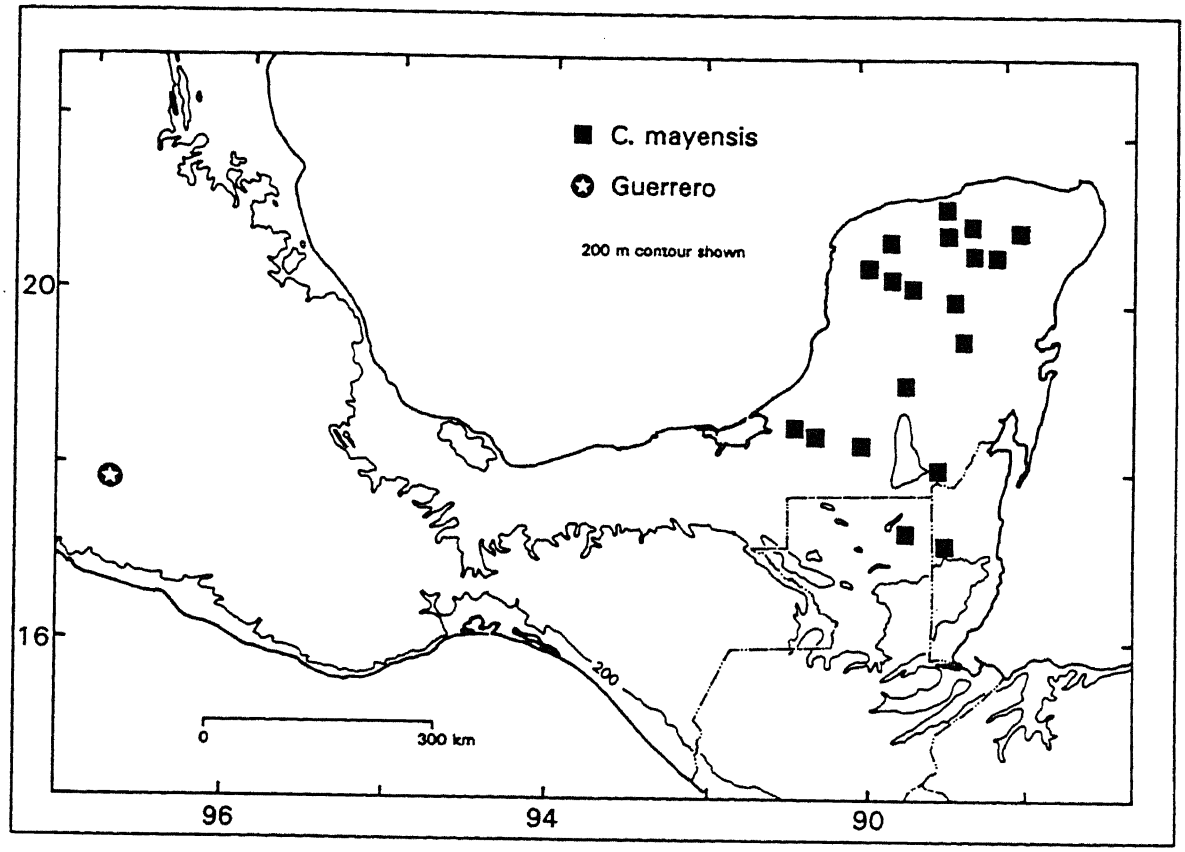

Fig. 30. Map of the distribution of C. mayensis.

Table 7. Selected measurements of members of the C. nigrescens group. Abbreviations of measurements are explained in Methods section of text. The statistics presented are mean ± standard deviation of the mean, and observed extremes. Number of individuals for each species is in parentheses.

Table 7

	C. mayensis	C. merriami	C. nigrescens	C. mera	Colombia
HB	70 ± 8 62 - 90 (10)	69 ± 4 60 - 77 (23)	68 ± 7 55 - 83 (70)	69 ± 2 67 - 73 (6)	76
TL	28 ± 3 24 - 33 (10)	29 ± 4 22 - 38 (23)	29 ± 4 19 - 37 (70)	27 ± 2 24 - 31 (6)	27
CBL	19.0 ± 0.4 18.2 - 19.6 (9)	19.4 ± 0.4 18.7 - 20.0 (16)	18.6 ± 0.7 16.9 - 20.2 (70)	18.3 ± 0.4 17.7 - 18.7 (6)	19.9
BB	9.2 ± 0.4 8.8 - 9.8 (8)	9.6 ± 0.2 9.2 - 10.0 (18)	9.2 ± 0.4 8.0 - 10.3 (70)	9.4 ± 0.3 9.1 - 9.8 (6)	10.0
ZB	2.3 ± 0.1 2.0 - 2.5 (21)	2.3 ± 0.2 2.0 - 2.6 (21)	2.0 ± 0.2 1.5 - 2.5 (70)	2.0 ± 0.1 1.9 - 2.2 (6)	2.0
PO	4.4 ± 0.2 4.1 - 4.8 (21)	4.7 ± 0.1 4.4 - 4.9 (21)	4.4 ± 0.2 3.9 - 4.9 (70)	4.5 ± 0.2 4.3 - 4.7 (6)	4.9
U1B	2.6 ± 0.1 2.2 - 2.7 (21)	2.6 ± 0.2 2.1 - 2.8 (21)	2.4 ± 0.2 2.1 - 2.8 (70)	2.5 ± 0.1 2.4 - 2.6 (6)	2.6
U3B	3.0 ± 0.1 2.8 - 3.3 (21)	3.0 ± 0.2 2.7 - 3.1 (6)	2.8 ± 0.2 2.4 - 3.2 (70)	2.9 ± 0.1 2.7 - 3.0 (6)	3.2
M2B	5.5 ± 0.1 5.2 - 5.7 (21)	5.8 ± 0.2 5.2 - 6.2 (21)	5.5 ± 0.3 4.9 - 6.0 (70)	5.6 ± 0.1 5.5 - 5.8 (6)	6.3
PL	8.3 ± 0.3 7.8 - 9.0 (21)	8.4 ± 0.3 7.9 - 8.9 (21)	7.9 ± 0.3 7.2 - 8.8 (70)	7.8 ± 0.1 7.6 - 7.8 (6)	8.8
TRL	7.3 ± 0.2 6.9 - 7.8 (21)	7.4 ± 0.2 6.8 - 7.7 (21)	7.1 ± 0.3 6.4 - 7.8 (70)	7.1 ± 0.1 6.9 - 7.2 (6)	7.7

Table 7 (cont.)

	C. mayensis	C. merriami	C. nigrescens	C. mera	Colombia
UTR	2.7 ± 0.2 2.1 - 3.1 (21)	2.5 ± 0.1 2.2 - 2.7 (21)	2.4 ± 0.1 2.0 - 2.6 (70)	2.4 ± 0.1 2.3 - 2.5 (6)	2.5
MTR	5.0 ± 0.1 4.8 - 5.3 (21)	5.2 ± 0.2 5.0 - 5.5 (17)	5.2 ± 0.2 4.7 - 5.7 (70)	5.1 ± 0.6 5.1 - 5.2 (6)	5.8
M1W	1.7 ± 0.05 1.7 - 1.8 (21)	1.9 ± 0.1 1.7 - 2.0 (21)	1.8 ± 0.1 1.5 - 1.9 (70)	1.8 ± 0.05 1.8 - 1.9 (6)	1.8
LM	6.2 ± 0.2 5.8 - 6.8 (24)	6.5 ± 0.3 6.0 - 7.2 (21)	6.2 ± 0.3 5.5 - 6.9 (70)	5.9 ± 0.4 5.2 - 6.2 (6)	6.9
HCP	5.3 ± 0.3 4.8 - 5.7 (24)	5.0 ± 0.2 4.6 - 5.3 (21)	4.5 ± 0.3 4.0 - 5.0 (70)	4.5 ± 0.1 4.3 - 4.6 (6)	4.8
HAV	2.9 ± 0.1 2.7 - 3.2 (24)	2.9 ± 0.2 2.6 - 3.3 (21)	2.7 ± 0.2 2.3 -3.0 (70)	2.7 ± 0.1 2.6 - 2.8 (6)	2.9
HAC	3.9 ± 0.2 3.4 - 4.4 (24)	3.8 ± 0.2 3.5 - 4.3 (21)	3.7 ± 0.2 3.3 - 4.1 (70)	3.7 ± 0.1 3.6 - 3.8 (6)	4.1
BAP	3.1 ± 0.1 2.8 - 3.3 (24)	3.0 ± 0.1 2.6 - 3.2 (21)	2.9 ± 0.1 2.6 - 3.2 (70)	3.0 ± 0.1 2.9 - 3.1 (6)	3.1
AC3	4.8 ± 0.2 4.4 - 5.3 (24)	4.6 ± 0.2 4.3 - 4.9 (21)	4.5 ± 0.2 3.8 - 5.1 (70)	4.4 ± 0.1 4.3 - 4.6 (6)	4.9
LMT	5.5 ± 0.2 5.3 - 5.8 (24)	5.7 ± 0.2 5.3 - 5.9 (21)	5.6 ± 0.3 5.1 - 6.2 (70)	5.5 ± 0.1 5.4 - 5.7 (6)	6.0
Lm1	1.7 ± 0.1 1.6 - 1.9 (24)	1.8 ± 0.1 1.7 - 1.9 (21)	1.7 ± 0.1 1.6 - 1.9 (70)	1.8 ± 0.1 1.7 - 1.8 (6)	1.9

the right or left frontal, small to medium in size; a well developed foramen leading to a ventral extension of the sinus canal typically present posterior to the external capitular facet on one (8%, n = 62) or both (86%) sides of the skull; normally no foramen dorsal to external capitular facet (93%, n = 61); anterior process of the petromastoid low and very narrow (Fig. 31A); paroccipital process prominent; zygomatic plate broad in proportion to CBL (11.8% ± 0.7, n = 10) and PL (27.8% ± 1.6, n = 72); anterior border of zygomatic plate from parastyle/mesostyle valley to mesostyle of M1, posterior border from metastyle of M2 to middle of M3, and from posterior one-third of base of maxillary process to posterior to maxillary process; palate long and narrow; upper toothrow crowded; unicuspids massive; U4 normally displaced medially, so that U3 and P4 in contact or nearly so; U4 not visible in lateral view of skull; lateral view of U3 also sometimes partially obstructed by P4; posterior borders of P4, M1, M2 unrecessed or only very slightly recessed; M3 with well-developed paracrista and paracone, reduced precentrocrista, poorly developed and normally uncolored mesostyle and protocone, and hypocone absent or vestigial and incorporated into the posterior cingulum; dentition bulbous.

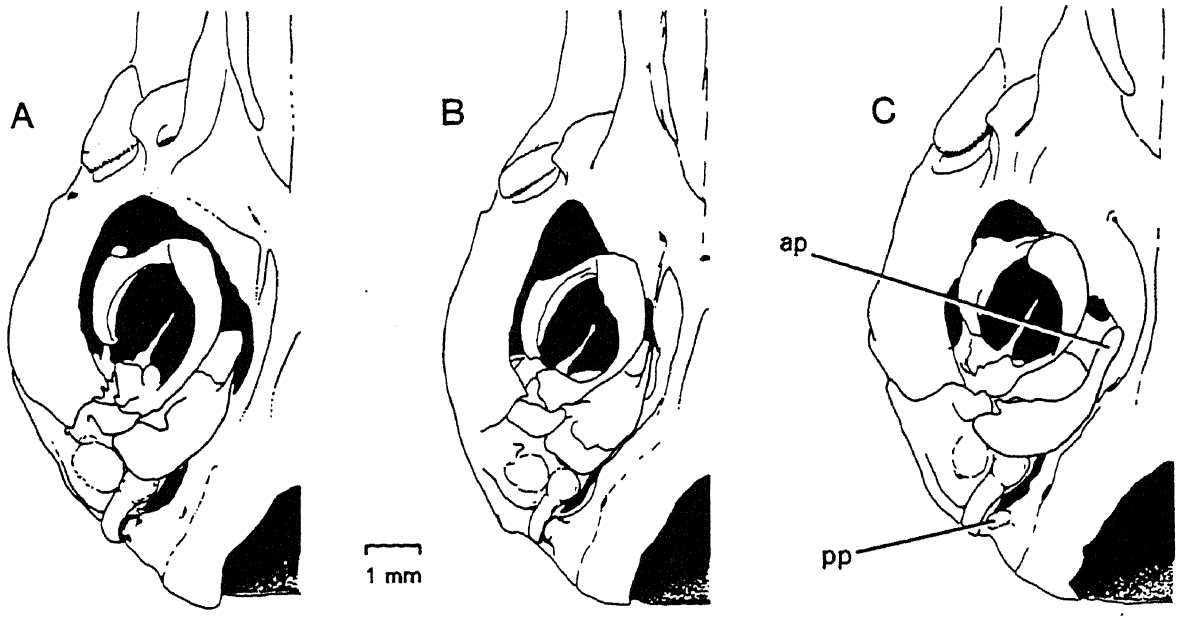

Figure 31. Ventral view of the right tympanic region of the skulls of C. merriami (A; UMMZ 117845), C. nigrescens (B; KU 143385), and Cryptotis "D" (C; FMNH 69816), illustrating the location and relative development of the anterior process of the petromastoid (ap) and the paroccipital process (pp).

Mandible large; horizontal ramus deep; coronoid process high (HCP/LM = 84.3% ± 3.3, n = 21) and broad, joins mandible at steep angle; viewed posteriorly, horizontal and vertical branches of articular condyle short and broad; lower sigmoid notch very shallow, not extending beneath ventral border of articular process; posterior border of lower incisor extends nearly to posterior border of cingulum of p4; lower dentition wide; only hypoconid in talonid of m3.

Remarks.--Cryptotis mayensis has the lightest pelage of any member of the genus, including C. parva, from which the coloration differs in being more gray and less olive. Overall appearance of C. mayensis is a medium brownish gray. Close inspection of the dorsal pelage of C. mayensis reveals that the individual hairs are three-banded. The proximal one-half to three-quarters of the hairs is a medium gray, followed by a narrow band of light gray. The distal tip (about one-eighth of the total length) of the hair is brownish-gray. The transition between bands is not sharp, the colors tending to grade into each other. The great extent of lighter, basal coloration in the hairs of this taxon probably accounts for its overall lighter appearance and greater reflectance.

Goldman (1951) described the northern Yucatan habitat

around Chichén Itzá, from which the holotype of C. mayensis was collected, as stunted tropical forest about 25 to 40 ft. high with dense, brushy undergrowth. He noted that the weather is highly seasonal, with a long, hot, dry season from about December to June and a rainy season marked by torrential afternoon showers. Dowler and Engstrom (1988) reported a specimen from 7.5 km W Escárcega, Campeche, as having been trapped in mature, transitional deciduous-evergreen forest. In the same area they also collected Heteromys gaumeri, Ototylomys phyllotis, Peromyscus yucatanicus, and Oryzomys melanotis. Alvarez and Martinez (1967) captured a C. mayensis along a road in tropical rain forest opposite a corn field, 2 km SE Laguna Chickankanaab, Quintana Roo.

Few reproductive data are available for C. mayensis, and no pregnant or lactating females have been recorded. Males captured on 4 June, 24 June, and 19 August showed no indications of having lateral glands. When present, these paired glandular areas lack long guard hairs and underfur, but have a sparse covering of short, fine hairs (Woodman and Timm, submitted; manuscript). Both males and females possess lateral glands, but in females they are much smaller and more difficult to see (Murariu, 1976; Bee et al., 1980). It is likely that these glands serve a function in sexual communication.

Eadie (1938) found that the lateral glands of male Blarina showed increased activity with enlargement of the testes.

Cryptotis mayensis is rarely collected, and there are few complete specimens in museum collections. However, it is unlikely that this shrew is truly rare, because remains from owl pellets are abundant. Of 121 specimens examined in our study 76 came from owl pellets, 33 are from archeological contexts, and 12 are standard museum specimens.

Cryptotis mayensis is distinctive in being the only member of the genus restricted to lowland areas. In the Yucatan Peninsula the species is not known to occur above 100 m. The only specimens of C. mayensis from outside of the Yucatan Peninsula are crania and unassociated mandibles collected by William López-Forment C. in 1969 from below a barn owl (Tyto alba) roost in Macuiltzingo Cave [Cueva del Cañon de Zopilote], located at 650 m in the Cañon de Zopilote, Guerrero, Mexico (Choate, 1970). The precise locality and habitat where the shrews were captured by owls remains unknown, and subsequent work in Macuiltzingo Cave has not produced additional specimens (López-Forment and Urbano, 1977; W. López-Forment C., pers. comm.), suggesting a change in feeding patterns by the

owls or local extinction of the population of shrews upon which they were feeding. When one of us (Woodman) visited the cave with W. López-Forment C. in August 1991, no owls were occupying the cave, and there was no evidence of any recent use of the cave by owls. Despite repeated collecting in the region surrounding the cave (Choate, 1970; W. Lopez-Forment C., pers. comm.; field work by Woodman in 1991), no additional specimens of these shrews have been obtained.

The presence of shrews identifiable as C. mayensis in Guerrero presents an interesting biogeographical problem. These shrews are from an area that clearly is isolated geographically from the Yucatan Peninsula and is climatically and vegetationally distinct. Choate (1970) noted the great distance (> 950 km) and extensive biogeographical barriers between Zopilote Canyon and the nearest known locality of C. mayensis on the Yucatan Peninsula and suggested that the specimens from Zopilote Canyon eventually might prove to be subspecifically distinct. All known specimens from Guerrero are mandibles and incomplete skulls, making comparisons with other taxa, including C. mayensis difficult.

One specimen from Guerrero (IBUNAM 11039) has an auxiliary unicuspid (RU5 or a second RU4) in the upper right unicuspid toothrow. Supernumerary unicuspids

previously have been reported for Blarina (Choate, 1968), but this appears to be a fairly rare dental abnormality in soricids. It is much more common for individuals to lack unicuspids (Choate, 1968, 1970).

If more complete specimens of the Guerreran shrews become available, they may show that this population represents a distinct species.

Cryptotis merriami J. R. Choate, 1970

Fig. 31A, 32

Cryptotis nigrescens merriami J. R. Choate, 30 December 1970, Univ. Kansas Pubs. Mus. Nat. Hist. 19:277; E. R. Hall, 3 April 1981, The Mammals of North America 1:63.

Cryptotis nigrescens G. G. Goodwin, 29 May 1942, Bull. Amer. Mus. Nat. Hist. 79:117; W. H. Burt and R. A. Stirton, 22 September 1961, Misc. Pubs., Mus. Zool., Univ. Michigan 117:21.

Cryptotis parva orophila J. R. Choate, 30 December 1970, Univ. Kansas Pubs. Mus. Nat. Hist. 19:262 (part); E. R. Hall, 3 April 1981, The Mammals of North America 1:61 (part).

Cryptotis nigrescens nigrescens J. R. Choate, 30

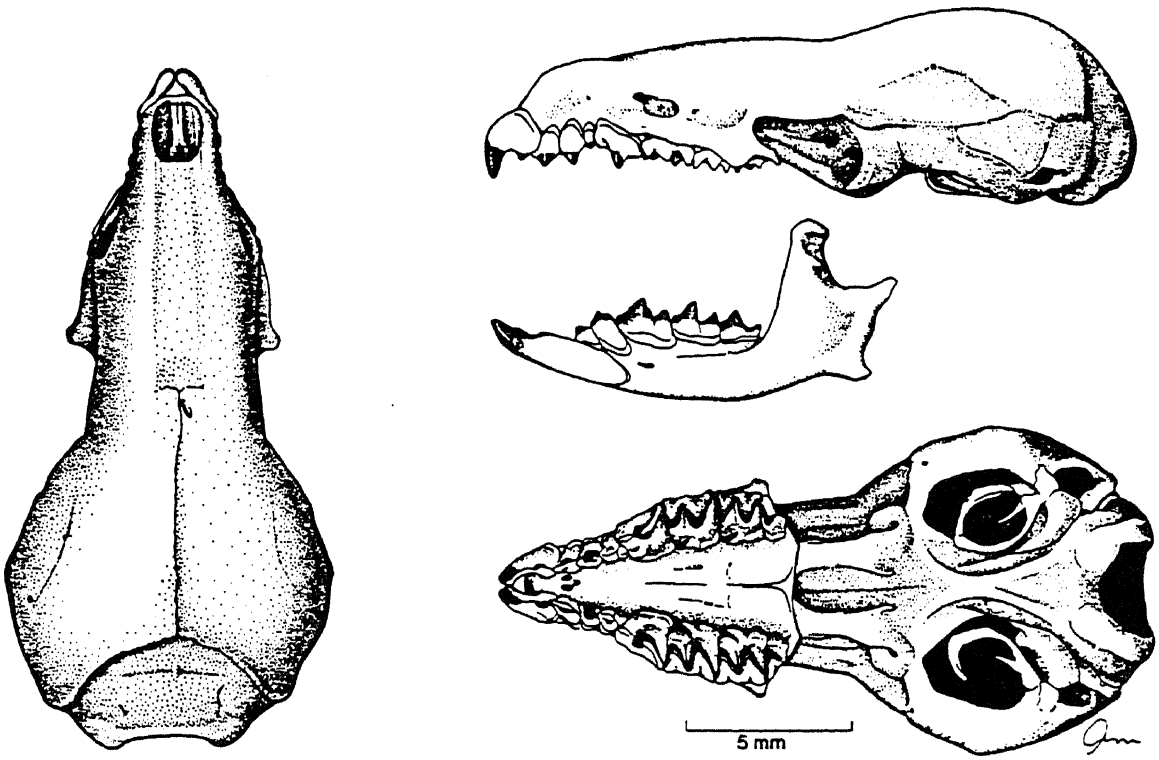

Fig. 32. Dorsal, ventral, and lateral views of the skull and lateral view of the skull and mandible of C. merriami (MVZ 130335).

December 1970, Univ. Kansas Pubs. Mus. Nat. Hist. 19:279 (part); E. R. Hall, 3 April 1981, The Mammals of North America 1:63 (part).

Holotype.--Skin and skull of adult female, U.S. National Museum of Natural History no. 77050, obtained by E. W. Nelson and E. A. Goldman (collector number 8846) 21 December 1895 from Guatemala, Huehuetenango, Jacaltenango, 5400 ft.

Distribution.--Cryptotis merriami occurs in the highlands of Chiapas, Guatemala, Honduras, El Salvador, and northern Nicaragua, with a disjunct population in the Tilarán Highlands of Costa Rica (Fig. 33). Known elevational distribution is from 975 to 1650 m.

Description.--A medium size Cryptotis, HB averaging 69 (Table 7); tail short, averaging 43% (± 1, n = 23) of head and body length; dorsal hairs usually about 4 mm long, ranging from 3 to 5 mm long, two-banded; dorsal and lateral pelage may be Olive Brown, Mummy Brown, or Clove Brown; venter is slightly lighter than dorsum, Buffy Brown or Olive Brown.

Rostrum broad and moderately long (PL/CBL = 43.4 ± 1.0, n = 16); interorbital area very broad; usually only one dorsal foramen (76%, n = 21), normally located on the

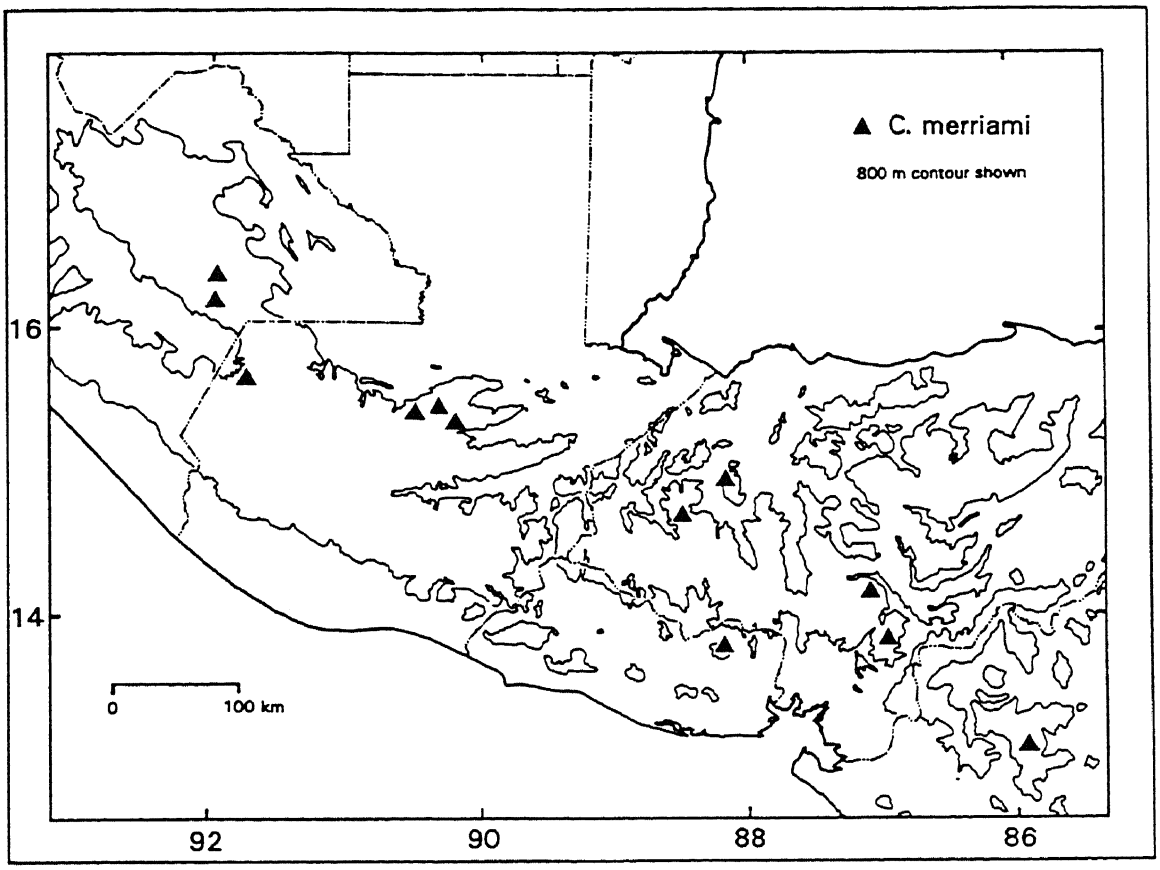

Fig. 33. Map of the distribution of C. merriami.

right frontal, medium to very large in size; a well developed foramen typically present posterior to the dorsal articular facet on one (10%, n = 10) or both (70%) sides of the skull; normally no foramen dorsal to external capitular facet (70%, n = 10); anterior process of the petromastoid low and very narrow (Fig. 31A); paroccipital process prominent; zygomatic plate broad in proportion to CBL (12.0% ± 0.8, n = 16) and PL (27.5% ± 2.1, n = 23); anterior border of zygomatic plate from posterior one-half of parastyle/mesostyle valley to mesostyle of M1, posterior border from posterior one-half of mesostyle/metastyle valley of M2 to middle of M3, and from middle of base of maxillary process to posterior to maxillary process; palate wide; upper toothrow crowded; unicuspids massive; U4 normally displaced medially, so that U3 and P4 in contact or nearly so; U4 not visible in lateral view of skull; lateral view of U3 also sometimes partially obstructed by P4; posterior borders of P4, M1, M2 unrecessed or only very slightly recessed; M3 with well-developed paracrista, and paracone, reduced precentrocrista, poorly developed and normally uncolored mesostyle and protocone, hypocone absent or vestigial and incorporated into the posterior cingulum; upper dentition quite bulbous.

Mandible large; horizontal ramus deep; coronoid process high (HCP/LM = 76.8% ± 3.5, n = 16) and broad, joining mandible at a steep angle; horizontal and vertical branches of articular condyle short and broad; lower sigmoid notch very shallow; posterior border of lower incisor extends almost to posterior border of cingulum of p4; lower dentition wide and long; only hypoconid in talonid of m3.

Comparisons.--C. mayensis: C. merriami is approximately the same in overall size, but has a darker pelage, which is dark brown in appearance rather than grayish brown; skull is much wider overall, especially the rostrum, interorbital area, braincase, and palate; upper dentition much broader; longer mandible; shorter coronoid process.

Remarks.--The dorsal pelage of C. merriami is indistinctly two banded. The proximal five-sixths of the dorsal hairs is a medium steel gray; the distal tip is medium brown. In two specimens from Guatemala (UMMZ 117844, 117845), the pelage is darker overall than those from El Salvador. The tips of the hairs of the Guatemala specimens are a darker brown.

Two specimens of C. merriami merit discussion. A male (UMMZ 117111) from Santa María de Ostuma,

Nicaragua, is the first specimen of the C. nigrescens complex to be identified from that country. This specimen was identified previously as C. parva orophila (Choate, 1970). A specimen of unknown sex from 4.5 km NE Tilarán (KU 84365) is the first record of this species from Costa Rica. It previously was referred to C. n. nigrescens (Choate, 1970). Both specimens display the large size, wide skull, broad zygomatic plate, robust mandible, and bulbous dentition characteristic of C. merriami. For this reason, we refer both to this species. They clearly are not referable to C. nigrescens or C. parva orophila. However, both specimens come from regions that are isolated geographically from the main range of C. merriami in Chiapas and northern Central America, and further study of larger series of specimens of this group may prove the shrews from Nicaragua and Costa Rica to be distinct. In addition, C. merriami and C. nigrescens may be sympatric or parapatric in parts of Costa Rica's Tilarán Cordillera.

Specimens of C. merriami from Cerro Cacaguatique, El Salvador, are geographically isolated from the main range of the species. However, the lack of any morphological differentiation between specimens from Cerro Cacaguatique and other parts of the range argues

against their being considered different taxa at this time.

The habitat on Cerro Cacaguatique, as noted by Burt and Stirton (1961) was oak forest with scattered pines from about 3500 ft [1065 m] up. Below that elevation, much of the area had been cleared for cultivation of coffee, bananas, and corn. Near the summit at 4000 ft [1220 m], epiphytes, ferns, and mosses occurred. Burt and Stirton (1961) reported taking C. merriami with Heteromys desmarestianus, Ototylomys phyllotis, and Peromyscus mexicanus along the rocky canyon slopes near the bottom, but specimens tags indicate that the shrews were taken from 3500 ft to the summit.

Goldman (1951) described the type locality of C. merriami as an indigenous village at an elevation of about 5400 ft [1645 m] and a little below the transition between the Humid Upper Tropical and Lower Austral or Upper Austral Life Zones. The locality is near the lower limit of cypress (Cupressus), but much of the region already had been deforested for cultivation of crops.

Few reproductive data are available for C. merriami, and no pregnant or lactating females have been recorded. Individual males collected on 23 May and 26 November had well-developed lateral glands. Two males captured on 2

January and 17 December, respectively, had no evidence of glandular development

Cryptotis nigrescens (J. A. Allen, 1895)

Fig. 31B, 34

Blarina (Soriciscus) nigrescens J. A. Allen, 8 November 1895, Bull. Amer. Mus. Nat. Hist. 7:339.

Blarina micrura J. A. Allen, 22 September 1893, Bull. Amer. Mus. Nat. Hist. 5:238.

Blarina nigrescens C. H. Merriam, 31 December 1895, N. Amer. Fauna 10:31.

C[ryptotis] nigrescens G. S. Miller, Jr., 31 October 1911, Proc. Biol. Soc. Washington 24:222.

Cryptotis nigrescens G. G. Goodwin, 10 December 1944, Amer. Mus. Novitates 1267:1; G. G. Goodwin, 31 December 1946, Bull. Amer. Mus. Nat. Hist. 87:288; H. W. Setzer, 29 September 1950, J. Washington Acad. Sci. 40:300; E. R. Hall and K. R. Kelson, 31 March 1959, The mammals of North America 1:63 (part); C. O. Handley, Jr., 22 November 1966, Checklist of the mammals of Panama, in Ectoparasites of Panama, p. 756.

Cryptotis zeteki H. W. Setzer, 29 September 1950, J.

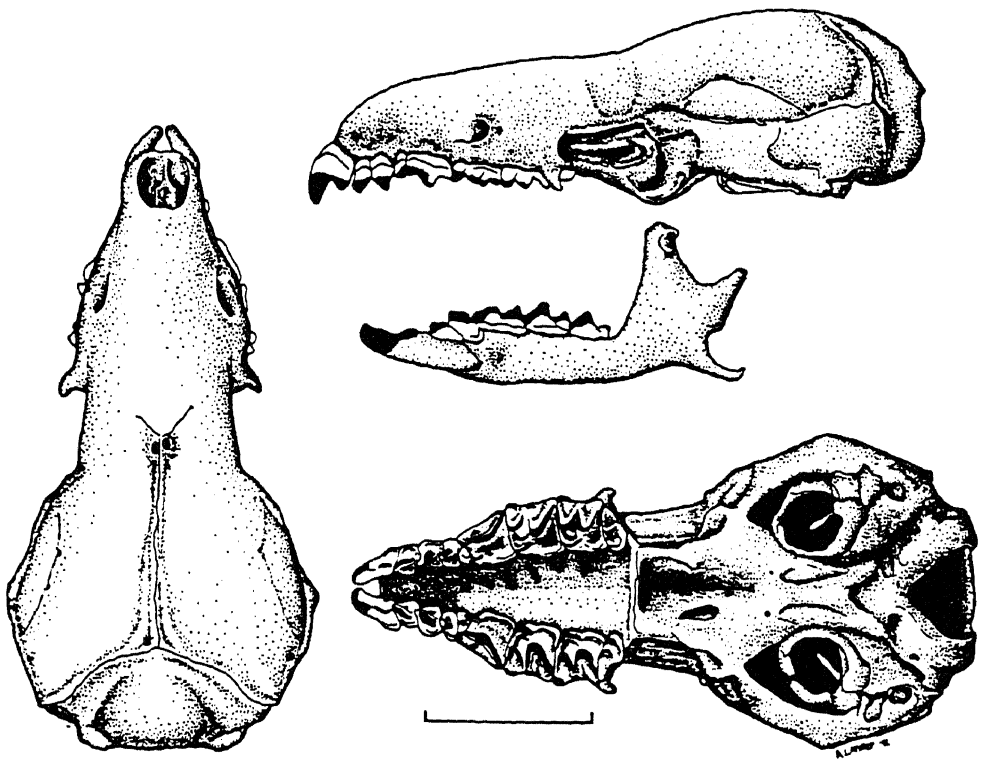

Figure 34. Dorsal, ventral, and lateral views of the skull and lateral view of the skull and mandible of C. nigrescens (KU 143389).

Washington Acad. Sci. 40:299; G. G. Goodwin, 28 June 1954, Amer. Mus. Novit. 1677:2; E. R. Hall and K. R. Kelson, 31 March 1959, The mammals of North America 1:62.

Cryptotis tersus G. G. Goodwin, 28 June 1954, Amer. Mus. Novit. 1677:1; E. R. Hall and K. R. Kelson, 31 March 1959, The mammals of North America 1:64.

Cryptotis nigrescens zeteki C. O. Handley, Jr., 22 November 1966, Checklist of the mammals of Panama, in Ectoparasites of Panama, p. 756.

Cryptotis parva orophila J. R. Choate, 30 December 1970, Univ. Kansas Pubs. Mus. Nat. Hist. 19:262 (part).

Cryptotis nigrescens nigrescens J. R. Choate, 30 December 1970, Univ. Kansas Pubs. Mus. Nat. Hist. 19:279 (part); E. R. Hall, 3 April 1981, The mammals of North America 1:63 (part).

Holotype.--Skin and skull of subadult, sex unknown, American Museum of Natural History no. 9591/7952, collected by G. K. Cherrie (collector number 2004) 5 September 1891 from Costa Rica, San José Province, San Isidro.

Distribution.--Occurs in highlands above 800 m in Costa

Rica and western Panama (Fig. 35). In Costa Rica, C. nigrescens is known from the Tilarán, Central, and Talamanca cordilleras; in Panama, it is known from the Chiriquí Cordillera. The known elevational distribution in Costa Rica is from 870 m to 2865 m; in Panama, it is 820 m to 2150 m.

Description.--A small to medium Cryptotis, HB averaging 68 (Table 7); tail short, averaging 43% (± 5, n = 70) of head and body length; snout in fluid-preserved specimens short and broad; dorsal hairs approximately 4.5 mm long, ranging from 4 to 5 mm, two-banded; pelage coloration varies somewhat geographically; dorsal and lateral pelage Mummy Brown or Clove Brown; ventral pelage slightly lighter, Buffy Brown, Saccardo's Umber, Olive Brown, or Mouse Gray.

Rostrum narrow and of normal length (PL/CBL = 42.6% ± 0.8, n = 70); interorbital area of moderate breadth; often two dorsal foramina (68%, n = 59), small to large size, positioned close to suture between frontals; normally no foramen posterior to the external capitular facet (88%, n = 57); usually a well developed foramen dorsal to external capitular facet on one (2%, n = 57) or both sides of the skull (93%), but foramen may be minute (3%); anterior process of the petromastoid very

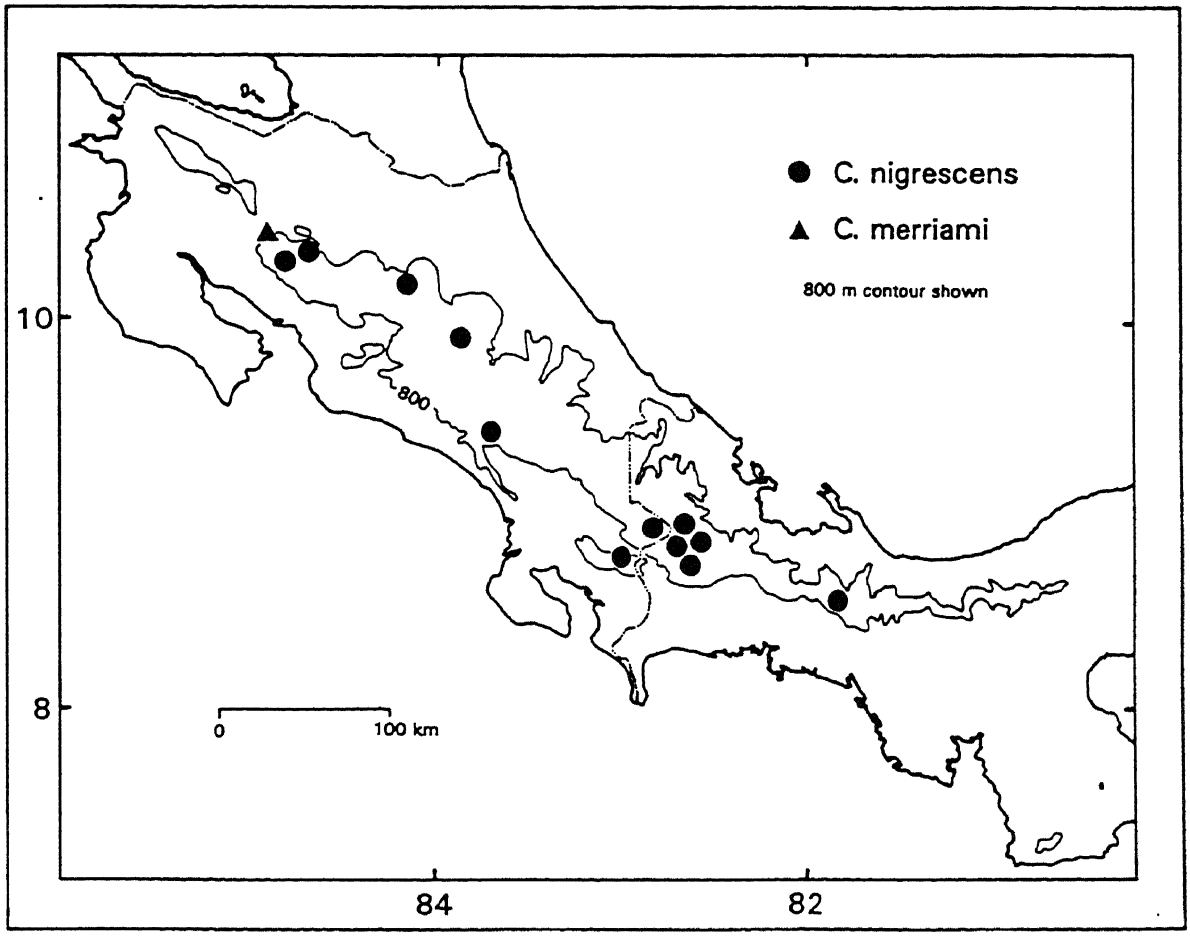

Figure 35. Map of the distribution of C. nigrescens.

low and very narrow (Fig. 31B); paroccipital process prominent; zygomatic plate narrow in proportion to CBL (10.5% ± 0.9, n = 75) and PL (24.8% ± 2.1); anterior border of zygomatic plate from mesostyle to mesostyle/metastyle valley of M1, posterior border at posterior one-half of mesostyle/metastyle of M2 to middle of M3, and usually at middle of base of maxillary process, but can occur from anterior one-half of this process to posterior to the process; palate moderately wide; upper toothrow not especially crowded; U4 normally in line of unicuspid toothrow, preventing contact between U3 and P4; U4 usually obscured by P4 in lateral view, but often partly visible; posterior borders of P4, M1, M2 unrecessed or only slightly recessed; M3 with well-developed paracrista, and paracone, reduced precentrocrista and mesostyle, poorly developed, but often colored postcentrocrista and metacone (but postcentrocrista short with mesostyle and metacone closely associated), protocone present and often colored, poorly developed hypocone often present; dentition not bulbous.

Mandible of moderate length and breadth; coronoid process low (HCP/LM = 71.7% ± 2.6, n = 70) and narrow, joins mandible at a steep angle; articular condyle relatively short and narrow; lower sigmoid notch very

shallow; posterior border of lower incisor almost to posterior border of cingulum of p4; vestigial entoconid occasionally present (38%, n = 50) in talonid of m3.

Comparisons.--Cryptotis nigrescens is the only member of the C. nigrescens complex sometimes possessing an entoconid in the talonid of m3.

Cryptotis mayensis: C. nigrescens has a much darker pelage, dark brown in appearance rather than grayish brown; skull is less robust; rostrum not as broad; anterior process of the petromastoid lower; foramen associated with ventral branch of sinus canal normally absent; foramen dorsal to dorsal articular facet of skull normally present; much more likely to have two dorsal foramina, one on each frontal; relatively and absolutely narrower zygomatic plate, anterior border of which is positioned more posteriorly relative to upper toothrow; palate relatively wider; upper dentition not as massive, unicuspids not as broad; upper molars relatively longer; unicuspid toothrow less crowded; mandible relatively longer and more slender; coronoid process shorter and narrower; branches of articular process narrower; lower molars relatively longer; hypoconid sometimes present on m3.

Cryptotis merriami: C. nigrescens has a generally darker

pelage; skull is not nearly as robust, much narrower overall, especially the rostrum, interorbital area, braincase, and palate; anterior process of the petromastoid lower; relatively and absolutely narrower zygomatic plate, anterior border of which is positioned more posteriorly relative to upper toothrow; upper dentition absolutely smaller, narrower, less massive; unicuspid row generally less crowded; M3 slightly more developed, possessing minute postcentrocrista and metacone; mandible shorter and more slender; coronoid process shorter and narrower; branches of articular process narrower; lower molars narrower; hypoconid sometime present on m3.

Remarks.--Viewed anteriorly, the pelage of C. nigrescens is very reflective. The resulting sheen distorts the hues making colors appear lighter, especially on the ventrum. Dorsal pelage of C. nigrescens appears two-banded. The proximal three-quarters of the hairs is medium steel gray; the remaining distal portion is dark brown. In general, specimens from Costa Rica have slightly darker pelage, from Mummy Brown to Bone Brown and Clove Brown dorsally with a Buffy Brown or Olive Brown venter. Specimens from western Panama are Mummy Brown dorsally with a venter of Buffy Brown, Saccardo's

Umber, or Sepia in the Chiriquí highlands. The darkest specimens are two shrews (USNM 520692, 520693) from Fish Camp, Bocas del Toro Province, Panama, which are Blackish Brown-2 dorsally and Deep Grayish Olive ventrally. They are in contrast to the slightly lighter specimens from other localities in western Panama. These two specimens from Fish Camp also have very long tails (52-53% of head and body length). However, both are young animals with nearly unworn dentition, and this may account for the differences between them and other C. nigrescens from Panama.

There is a fair amount of variation between the large series of C. nigrescens from Monteverde, Costa Rica, and those from near San Félix (including Cerro Bollo), Panama. Specimens from Monteverde and from San Félix differ greatly in size (Table 7). In addition, the presence of a hypoconid on m3 is much more prevalent in the Panamanian series (71%, n = 14) than in the Monteverde specimens (25%, n = 32), and two dorsal foramina are present more often in specimens from near San Félix (94%, n = 16) than in those from Costa Rica (58%, n = 43). Further collecting and study of Cryptotis from Panama and Costa Rica may show that C. nigrescens is a complex of species.

Specimens of C. nigrescens from Cinchona and

Monteverde, Costa Rica, and from Santa Clara and Boquete Trail on Cerro Punta, Panama, previously were identified as C. parva orophila (Choate, 1970). The small size of Costa Rican C. nigrescens and the simple M3 can make the two species difficult to tell apart. Cryptotis nigrescens can be distinguished by its much darker pelage coloration, on both venter and dorsum, and by its relatively longer tail. In addition, C. nigrescens has a longer zygomatic plate, the posterior margins of P4, M1, and M2 are not as deeply recessed, M3 possesses a reduced metacone, and there is sometimes a hypoconid on m3. Our correction of these identifications means that C. parva presently is not known south of Costa Rica.

Setzer (1950) gives the location of Cerro Punta, the type locality of C. zeteki (a junior synonym of C. nigrescens) as 8°42'N, 82°48' W". Based on recent maps and gazetteers, the community is located at 8°34'N, 81°50'W.

Hall's (1981:63) map of the distribution of C. nigrescens implies that the species is found throughout Costa Rica, including low elevations along both coasts (with the exception of the Nicoya and Osa peninsulas), and throughout much of central and eastern Panama. Cryptotis nigrescens, as we understand it today, inhabits only higher elevations, and it is restricted to

the Tilarán, Central, and Talamanca cordilleras of Costa Rica and the Chiriquí Cordillera of Panama. At Monteverde the species occurs in cloud forest, forest fragments, and in pastures from 870-1660 m, and in western Panama it has been taken in cloud forest, disturbed cloud forest, elfin woodland, and drier Pacific slope forest from 1275-1856 m. The known upper elevational range for C. nigrescens is 2865 m. This probably approaches the true upper range for the species, because collections of shrews from higher elevations do not include this species. Cryptotis gracilis is known from 2435-3536 m in the Talamancan and Chiriquí highlands, and C. jacksoni, a member of the C. gracilis complex, has been taken from 2350-3180 m on Volcán Irazú. That this is not a simple case of competitive exclusion is suggested by the fact that C. nigrescens and C. gracilis overlap in their elevational range and that both have been collected from the same locality in Panama (R. Pine, pers. comm.).

In the Monteverde area, we found C. nigrescens in a variety of habitat types including Tropical Premontane Rain Forest, Tropical Premontane Moist Forest, Tropical Premontane Wet Forest, and Tropical Lower Montane Wet Forest. Common small mammals in these habitats include: Peromyscus nudipes, Heteromys desmarestianus, Scotinomys

teguina, and Reithrodontomys creper and Oryzomys albigularis at the higher elevations. A second species of small-eared shrew, C. monteverdensis occurs at the higher elevations in the Monteverde Cloud Forest (Woodman and Timm, submitted). Cryptotis monteverdensis is a much larger shrew and is a member of the C. gracilis complex. At this point, we can not say if these two species are truly syntopic, although they are sympatric in this area. Cryptotis nigrescens are probably abundant at Monteverde, but are difficult to capture. During several weeks' field work in 1989, we had over 1570 trapnights using a combination of Sherman live traps, Museum Specials, and common snap traps baited with a mixture of grease, seeds, raisins, and vanilla, and over 500 trapnights using pitfalls with drift fences. Of a total of 24 shrews we obtained, none were captured in baited traps, 8 were taken in our pitfalls, 5 more were captured in pitfalls set by entomologists in a study apart from ours, 3 were brought in by domestic cats, and 8 were encountered dead on a trail or road by local residents prior to our arrival.

Few reproductive data are available for C. nigrescens. A female (USNM 516623) from east of Cerro Pando was recorded as "recently lactating" on 16 March 1973, and a lactating female (USNM 516620) was collected

at Santa Clara on 25 March 1972. We captured an adult female (KU 143389) with 3 embryos (CR = 4 mm) at Monteverde on 12 May 1989 and another with an enlarged uterus on 21 May (KU 143396), suggesting that it had recently given birth. Two females (USNM 541044, 541030) pregnant with a single embryo each (CR = 15 mm, 5 mm) were taken on 2 and 4 July 1980, respectively, 24-24.5 km NNE of San Félix. Females without embryos have been captured from 9 - 23 May at Monteverde (n = 6) and on 13 June and 26 June in Panama (n = 2). Our inspection of male C. nigrescens show well-developed lateral glands on 20 individuals collected from 9 May through 1 July. Individual males without well-developed lateral glands were collected on 26 February, 7 March, 11 March, 3 April, 28 July, and 4 July. On 9 May and 18 May we recorded individual males from Monteverde with melanistic sheaths surrounding the testes; both animals had well-developed lateral glands and enlarged testes (3.5 x 2.5 mm, 4 x 2.5 mm, respectively).

A young adult female (KU 143393) captured at Monteverde on 15 May 1989 lacks digits on its right forefoot. The vestigial first digit is the only one bearing a claw, and this is poorly formed. The form of the foot suggests that the digits were never fully developed during ontogeny rather than lost later due to

an accident.

Cryptotis mera E. A. Goldman, 1912

Fig. 36

Cryptotis merus E. A. Goldman, 20 September 1912, Smiths. Misc. Coll. 60(2):17; E. A. Goldman, 24 April 1920, Smiths. Misc. Coll. 69(5):171; H. W. Setzer, 29 September 1950, J. Washington Acad. Sci. 40:300; G. G. Goodwin, 28 June 1954, Amer. Mus. Novit. 1677:2.

Cryptotis mera E. R. Hall and K. R. Kelson, 31 March 1959, The mammals of North America 1:61.

Cryptotis nigrescens mera C. O. Handley, Jr., 22 November 1966, Checklist of the mammals of Panama, in R. L. Wenzel and V. J. Tipton (eds.), Ectoparasites of Panama, p. 756.

Cryptotis nigrescens nigrescens J. R. Choate, 30 December 1970, Univ. Kansas Pubs. Mus. Nat. Hist. 19:279 (part); E. R. Hall, 3 April 1981, The mammals of North America 1:63 (part).

Holotype.--Skin and skull of a male, U.S. National Museum of Natural History no. 178976, collected by E. A. Goldman (original number 21669) 2 May 1912 from Panama, Darién Province, Mount Pirri [Cerro Pirre], near head of

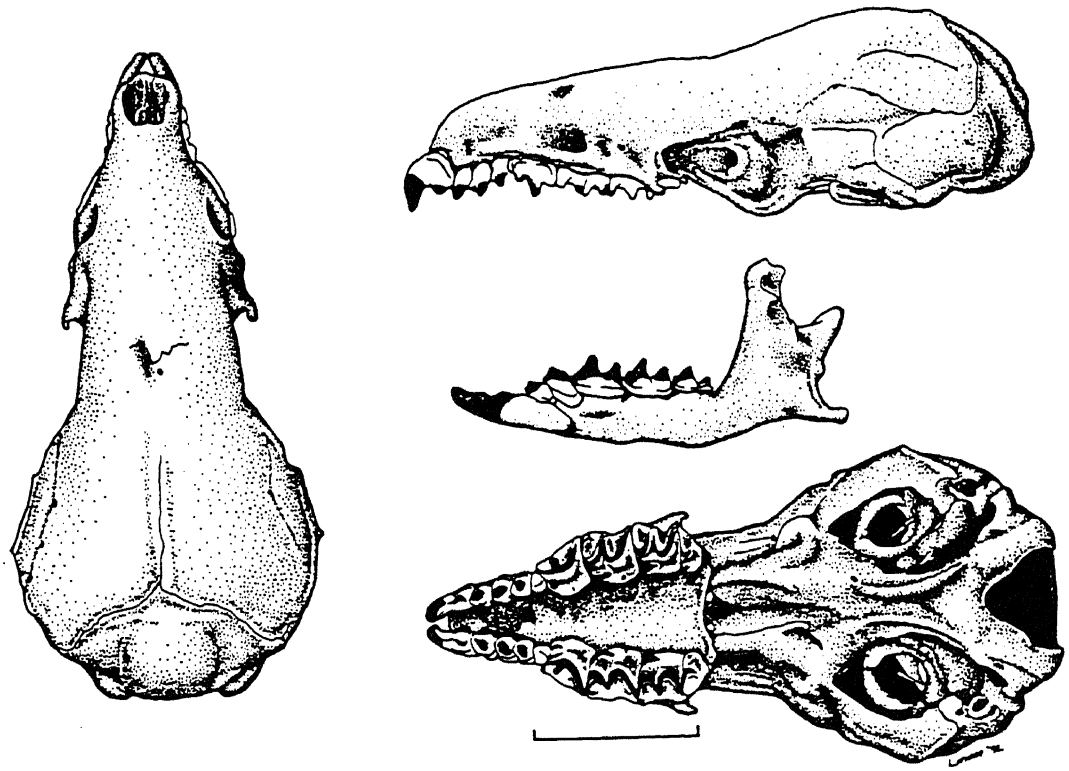

Figure 36. Dorsal, ventral, and lateral views of the skull and lateral view of the skull and mandible of C. mera (USNM 337969).

Río Limón, 4500 ft.

Distribution.--Cerro Tacarcuna and Cerro Malí in the eastern Serranía de Darién, and Cerro Pirre in the Serranía de Pirre (Fig. 37). The species undoubtedly occurs in Colombia, but all specimens currently known are from the Panamanian side of the border. The recorded elevational distribution of the species is 1370 to 1525 m.

Description.--A medium Cryptotis, HB averaging 69 (Table 7); tail short, averaging 39% (± 2, n = 6) of head and body length; dorsal hairs approximately 4 mm long, ranging from 3.5 to 4.5 mm, indistinctly two-banded; dorsal and lateral pelage Mummy Brown; ventral pelage slightly lighter, Saccardo's Umber or Mouse Gray.

Rostrum of normal length (PL/CBL = 42.4 ± 1.1, n = 5); interorbital area of moderate breadth; often 2 dorsal foramina (66%, n = 6), not normally equal in size, positioned close to suture between frontals; normally no foramen posterior to the external capitular facet (100%, n = 4); usually a well developed foramen dorsal to external capitular facet on both sides of the skull (75%, n = 4), but foramen may be minute (25%); anterior process of petromastoid very low and very narrow (Fig. 31B); paroccipital process prominent;

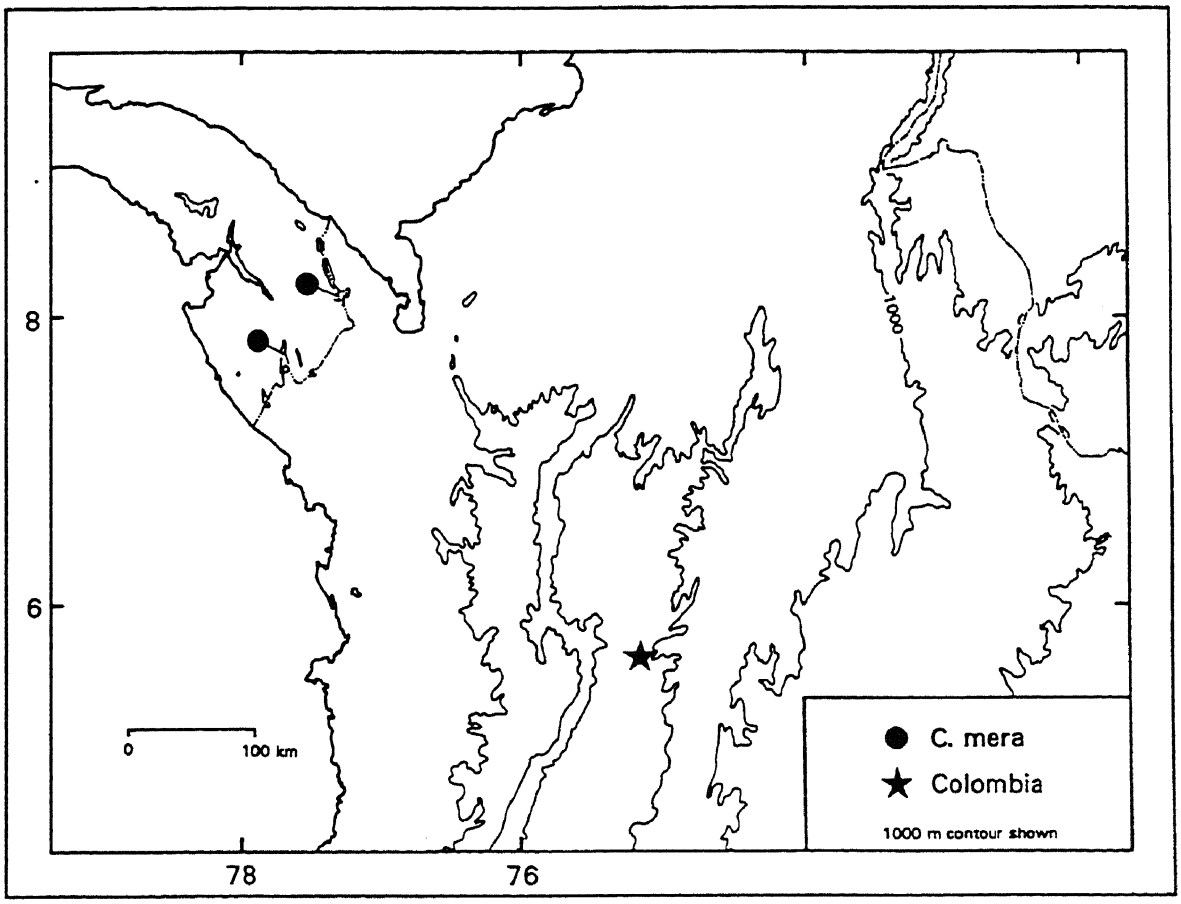

Figure 37. Map of the distribution of C. mera and the type locality of the new species from Colombia.

zygomatic plate narrow in proportion to CBL (11.0% ± 0.7, n = 5) and PL (26.0% ± 1.3, n = 6); anterior border of zygomatic plate at mesostyle/metastyle valley of M1, posterior border at metastyle of M2 to middle of M3, and from anterior edge to posterior edge of maxillary process; palate moderately wide; upper toothrow crowded; unicuspids massive; U4 normally dispaced medially, so U3 and P4 in contact or nearly so; U4 usually not visible in lateral view; lateral view of U3 also often partly obstructed by P4; posterior borders of P4, M1, M2 only slightly recessed; M3 with well-developed paracrista and paracone, reduced precentrocrista, mesostyle and postcentrocrista poorly developed and normally uncolored, protocone present and often colored, hypocone poorly developed, appearing as a posterior cingulum; dentition quite bulbous.

Mandible of moderate length and breadth; coronoid process high (HCP/LM = 76.3% ± 4.8, n = 6), but narrow, joins mandible at fairly steep angle; articular condyle relatively short and broad; lower sigmoid notch very shallow; posterior border of lower incisor almost to posterior border of cingulum of p4; only hypoconid in talonid of m3.

Comparisons.--*Cryptotis mayensis*: *C. mera* has a much darker pelage, dark brown in appearance rather than

grayish brown; skull is much shorter, but interorbital area much broader; palate relatively wider; anterior process of the petromastoid lower; foramen associated with ventral branch of sinus canal normally absent; foramen dorsal to dorsal articular facet of skull normally present; much more likely to have two dorsal foramina, one on each frontal; mandible more slender; coronoid process shorter and much narrower; lower molars relatively longer.

Cryptotis merriami: C. mera is much smaller in nearly all cranial dimensions; relatively broader palate; anterior process of the petromastoid lower; mandible not as deep; coronoid process much narrower.

Cryptotis nigrescens: C. mera has a relatively wider skull, especially in the interorbital area, and palate; relatively longer zygomatic plate; more crowded upper toothrow; relatively shorter, deeper mandible; no hypoconid on m3.

Remarks.--Choate (1970) considered C. mera a junior synonym of C. nigrescens nigrescens. At the time of his study, however, he had a total of only 29 specimens at hand. Recent collection of large series of C. nigrescens from Costa Rica and western Panama permitted

us to make more extensive comparisons, and we recognize C. mera as a distinct species.

Dorsal pelage of C. mera is two-banded, and is generallly similar to that of C. nigrescens from western Panama in color.

Cryptotis mera is known from cloud forest on two mountain areas isolated from each other by lowlands below 200 m. Specimens from the Serranía de Pirre have a shorter coronoid process (CP/LM = 71%, n = 2) than those from the Serranía de Darien (79% ± 3, n = 4), but are otherwise indistinguishable. Populations from these two areas may prove to be distinct once additional specimens are available, but at this time we consider them to be conspecific.

The holotype and two topotypes of C. mera were collected between 4500 to 5000 ft [1370 - 1525 m] in the Serranía de Pirre. Goldman (1912) described the region as covered with unbroken forest and having a seasonal, but very heavy annual rainfall. Although little actual rain falls during the dry season, clouds normally envelope the upper elevations, providing moisture year round.

Reproductive data for C. mera are scarce. Two females (USNM 337966, 337969) from Cerro Malí and Cerro Tacarcuna were lactating on 12 February and 11 March

1964, respectively.

Although Goldman (1912) orginally published this species name as "merus", the correct spelling is "mera". Cryptotis is feminine, dictating that the feminine ending be used on all adjectival species names used in combination with it (Woodman, in press).

Cryptotis "D"

Fig. 31C, 38

Holotype.--Skin and skull of adult female, Field Museum of Natural History no. 69816, collected 15 October 1950 by Philip Hershkovitz (original no. 4723). Skull nearly complete, but with a puncture hole in the dorsal braincase; skin in very good condition, but missing a small patch of fur on left venter, some fur stuck together.

Type locality.--Colombia; Central Cordillera; Antioquia Dept., Sonsón; 15 km E of Río Negrito; 1750 m.

Distribution.--At present, known only from type locality (Fig. 37).

Diagnosis.--A small to medium Cryptotis with very dark fur, a short tail, broad rostrum, palate, and interorbital area, foramen dorsal to dorsal articular facet but not posterior to this facet, narrow zygomatic

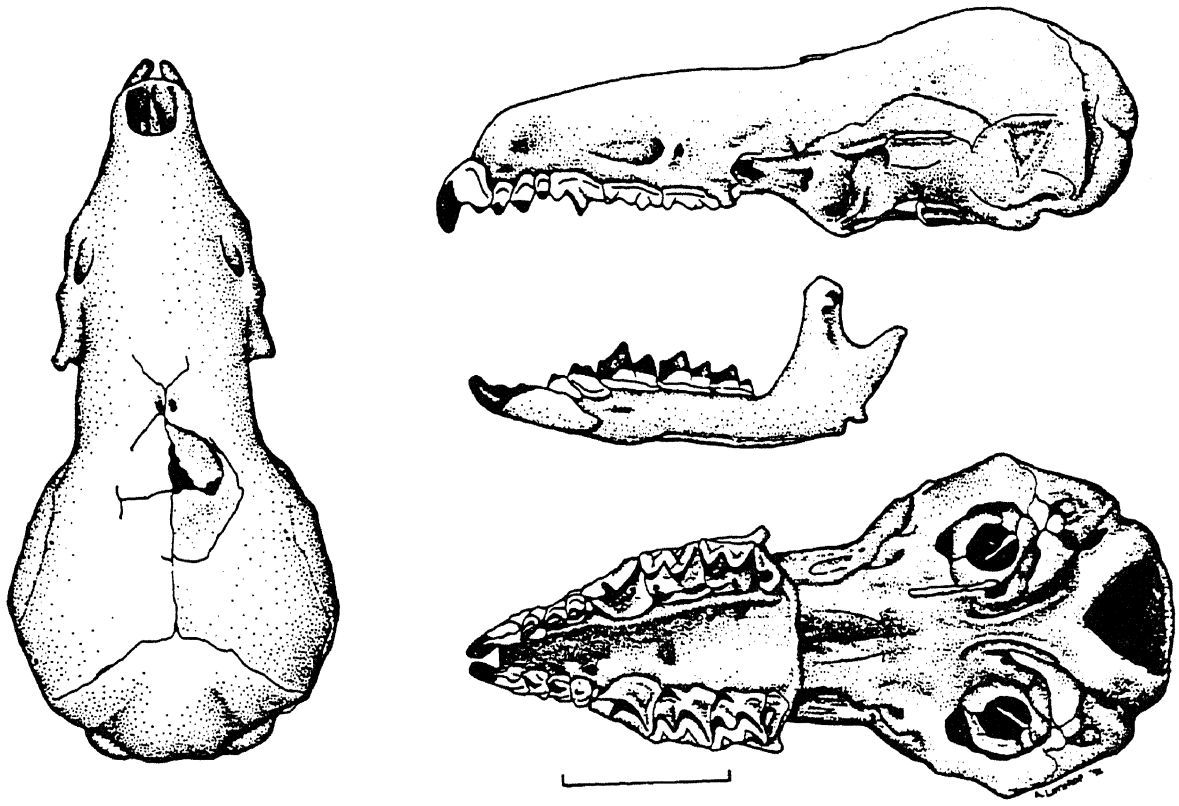

Figure 38. Dorsal, ventral, and lateral views of the skull and lateral view of the skull and mandible of Cryptotis "D" (FMNH 69816).

plate, crowded toothrow, bulbous and unrecessed dentition, simple M3, long mandible with a broad coronoid process that joins the horizontal ramus at nearly a right angle, short and broad articular condyle with no notch between the articular facets, shallow lower sigmoid notch, and lacking entoconid in talonid of m3.

Description of holotype.--A small to medium Cryptotis, HB = 76 (Table 7); tail short, 36% of head and body length; dorsal hairs approximately 4 to 5 mm long, two-banded; dorsal and lateral pelage Olive Brown to Fuscous; ventral pelage only slightly lighter, Buffy Brown to Hair Brown.

Rostrum broad and of normal length (PL/CBL = 44%); interorbital area broad; two large dorsal foramina, close to sagittal suture; no foramen posterior to the external capitular facet; a moderately well developed foramen dorsal to external capitular facet on both sides of the skull; anterior process of the petromastoid high and wide (Fig. 31C); paroccipital process low; zygomatic plate narrow in proportion to CBL (10.1%) and PL (22.7%); anterior border of zygomatic plate at posterior of mesostyle/metastyle valley of M1, posterior border at parastyle M3 and anterior to

posterior edge of base of maxillary process; palate wide; upper toothrow crowded; U4 reduced and peglike; U4 in line with other unicuspids, but too small to prevent contact between U3 and P4; U4 and corner of U3 obscured by P4 in lateral view; posterior borders of P4, M1, M2 only slightly recessed; M3 with well-developed paracrista, and paracone, reduced precentrocrista which joins the posterior cingulum; protocone of M3 poorly developed and uncolored; hypocone of M3 absent or part of posterior cingulum; dentition bulbous.

Mandible relatively long and of moderate breadth; coronoid process broad and low (HCP/LM = 69.6%) joining mandible at nearly a right angle; articular condyle distinctive: short and broad, lacking a lingual notch between the dorsal and ventral articular surfaces; lower sigmoid notch very shallow; posterior border of lower incisor almost to posterior border of posterior cingulum of p4; only hypoconid in talonid of m3.

Comparisons.--Cryptotis "D" is the largest of the five species in the C. nigrescens complex, and it differs from the other four in having a shorter tail, a much broader and higher anterior process of the petromastoid (Fig. 31); a lower, less prominent paroccipital process; narrower zygomatic plate, no notch between the facets of the articular condyle of the mandible; and low coronoid

process.

Cryptotis mayensis: Cryptotis "D" has a much darker pelage, dark brown in appearance rather than grayish brown; a moderately well developed foramen dorsal to the external capitular facet, but no foramen posterior to this facet; relatively shorter zygomatic plate; shorter unicuspid toothrow and longer molariform toothrow; broader interorbital area and much broader palate; smaller unicuspids; much shorter and much narrower coronoid process; longer mandible.

Cryptotis merriami.--Cryptotis "D" has a moderately well developed foramen dorsal to the external capitular facet, but no foramen posterior to this facet; wider palate; relatively shorter zygomatic plate; longer molariform toothrow; much shorter and narrower coronoid process; longer mandible.

Cryptotis nigrescens.--Cryptotis "D" differs in its much broader interorbital area and palate; longer molariform toothrow; somewhat broader coronoid process.

Cryptotis mera.--Cryptotis "D" has a broader interorbital area and somewhat broader palate; much longer molariform toothrow; shorter, broader coronoid process; longer mandible.

Remarks.--Cryptotis "D" is the only species of the C. nigrescens group which is known to occur in South America, although C. mera undoubtedly occurs in Colombia also. Both are considerably smaller than any other described South American Cryptotis, and they are also the only two South American shrews with a short, broad articular condyle, and a nearly right angle junction between the coronoid process and the body of the mandible. All other described species of Cryptotis from South America have a high, narrow articular process and a mandible with a wide internal angle between the coronoid process and the horizontal ramus. Cryptotis "D" is distinctive in being the only species known to lack a notch between the two articular facets of the articular condyle.

Cryptotis "D" is clearly more closely related to the C. nigrescens group than to any of the South American species. The occurrence of Cryptotis "D" on the Central Cordillera of Colombia suggests that it, or another, closely related species, is likely to occur at high elevations in the western Cordillera.

No reproductive data are available for Cryptotis "D".

Other species of mammals collected by Hershkovitz at the type locality of Cryptotis "D" include: Sciurus

pucheranii, Microxus bogatensis, Neacomys sp., Oryzomys albigularis, Rhipidomys sp., Reithrodontomys mexicanus, Thomasomys laniger, and Dasyprocta punctata.

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Specimens Examined

Specimens in the following list marked with an asterix (*) are cranial remains recovered from owl pellets. Those marked with a double asterix (**) are from archeological or paleontological sites.

Cryptotis "D" (1).--**COLOMBIA:** ANTIOQUIA: Sansón, 15 km E of Río Negrito, 1750 m (1 FMNH - holotype).

C. mayensis (121).--**BELIZE:** CAYO DISTRICT: Baking Pot (1 ROM); **MEXICO:** CAMPECHE: 60 km SE of Dzibalchen (19°10'N, 89°20'W) (1 ROM, 1 ASNHC); 7.5 km W of Escárcega (1 ASNHC); La Tuxpana Champoton [La Tuxpeña] (1 USNM); QUINTANA ROO: 2 km SE of Lago Chichencanab [spelled variously "Laguna Chickankanaab" (Alvarez and Martinez,

1967:205); "Laguna Chichancanab" (Choate, 1970:277; U.S. Board on Geographic Names, 1956)] (1 ENCB); 6 km S, 1.5 km W of Tres Garantías (1 ASNHC); YUCATAN: Actun Chacaljas (1 cranium** AMNH); Actun Coyok, 5-90 cm (2 crania, 8 right mandibles** AMNH); Actun Has, 0-85 cm (7 crania** AMNH); Actun Lara, 0-130 cm (5 crania** AMNH); Actun Oxkintok, 30-75 cm (3 left mandibles AMNH); Actun Spukil, owl perch (63 crania* AMNH); Actun Spukil, excavations (3 crania, 9 right mandibles** AMNH); Chichen Itzá (1 FMNH, 1 USNM - holotype); Chichen Itzá ["along the rim of the Xtolók cenote" (Hatt, 1938:334)] (1 AMNH); SW of Dzilan de Bravo (6* IBUNAM); Loltun (2* ASNHC); Lolton [Loltun], surface of cavern floor (3 crania, 4 left mandibles* AMNH); 6 km S Merida (1 KU); 13 km W Peto (1 KU*); Xbac (1 USNM).

Additional records.--**BELIZE:** CAYO DISTRICT: Baking Pot (Choate, 1970:277); **GUATEMALA:** PETEN: Uaxactún (Choate, 1970:277); **MEXICO:** YUCATAN: Buctzotz, Calotmul, Izamal, Nabalam, Senotillo, Temax, Tzalam, Valladolid, Xbac (Gaumer, 1917); Uxmal, Mayan ruins (Alvarez and Martinez, 1967:205; Choate, 1970:277).

Cryptotis cf. mayensis (39).--**MEXICO:** GUERRERO: Zumpango del Río District, Cañon del Zopilote, 11.5 km S of the Río Mescala bridge near Mescala; Cueva de Macuiltzingo (39* IBUNAM).

C. mera (7).--**PANAMA:** DARIEN: Cerro Tacarcuna, 4800 ft (3 USNM); Cerro Malí, 4700 ft (1 USNM); Mount Pirri [Cerro Pirre], E slope near head of Río Limón, 4500-5000 ft (3 USNM, including holotype).

C. merriami (29).--**COSTA RICA:** GUANACASTE: 4.5 km NE of Tilarán (1 KU). **EL SALVADOR:** MORAZAN: Mt. Cacaguatique, north slope, 3800-4000 ft (3 MVZ); SAN MIGUEL: Mt. Cacaguatique, 3500-4000 ft (8 MVZ; 2 UMMZ). **GUATEMALA:** ALTA VERAPAZ: La Primavera (1 AMNH); Tucurú, Hacienda Concepción, 1100 m (1 UMMZ); San Pedro Carchá (1 ENCB); HUEHUETENANGO: Barillas, Hacienda Santa Gregoria (1 UMMZ); Jacaltenango, 5400 ft (4 USNM - includes holotype). **HONDURAS:** EL PARAISO: Yuscaran, Monserrat [Cerro de Moncerrato], Cloud Forest (1 MCZ); FRANCISCO MORAZAN: La Tigre National Park, San Juancito, La Rosario (1 UNAH); LEMPIRA: Las Flores Gracias (1 AMNH); SANTA BARBARA: San José (1 AMNH). **MEXICO:** CHIAPAS: Volcán Kagchiná, 3.5 km N Las Margaritas, 1500 m (2 MHP*). **NICARAGUA:** MATAGALPA: 9 mi N of Matagalpa, Santa María de Ostuma, 1400 m (1 UMMZ).

Additional records: **EL SALVADOR:** AHUACHAPAN: 2 mi NW Apaneca (Burt and Stirton, 1961). **GUATEMALA:** ALTA VERAPAZ: La Primavera, 3200 ft (Choate, 1970:279). **MEXICO:** CHIAPAS: Cueva Los Llanos, 9 km S Las

Margaritas, 1500 m (Choate, 1970:279).

C. nigrescens (119).--**COSTA RICA:** ALAJUELA: Cinchona, 1600 m (1 KU); Monteverde Cloud Forest Reserve, 1580-1600 m (3 KU); Monteverde Cloud Forest Reserve, Peñas Blancas Valley, 870 m (2 KU); ALAJUELA/GUANACASTE border: Monteverde Cloud Forest Reserve, 1580 m (1 KU); CARTAGO: [Volcán] Irazú, 8000-9400 ft (1 AMNH); GUANACASTE/PUNTARENAS border: near Monteverde, Cerro Amigos, 1750-1790 m (3 KU); PUNTARENAS: Coto Brus [Canton], Sabalito District, Las Tablas, Río Cotón, 1700 m (1 MNCR); Monteverde, 1345-1600 m (3 FMNH, 1 INBio, 24 KU, 3 LACM, 1 MMNH, 7 UMMZ); Monteverde Cloud Forest Reserve, 1530-1660 m (5 KU); San Luis, 1200 m [ca. 2.5 km S Monteverde] (1 KU); 1 mi SW of Finca Las Cruces, San Vito, 4000 ft (3 LACM); SAN JOSE: San Isidro (1 AMNH - holotype); 9 mi N of San Isidro del General (Pan American Highway), 4800 ft (1 UMMZ). **PANAMA:** BOCAS DEL TORO: Fish Camp, 4900 ft (8°58'N, 82°40'W) (2 USNM); El Volcán [Hato del Volcán] (4 USNM); 19 km NNW of El Volcán, E of Cerro Pando, 8°56'30"N, 82°42'15"W, 6400 ft (1 USNM); Volcán de Chiriquí, Río Candela, 6000 ft (2 AMNH); 25 km NNE of San Félix, 1425-1500 m (5 USNM); BOCAS DEL TORO/CHIRIQUI border: Cerro Bollo, 3.5 km E Escopeta, which latter is at ca. 23 km NNE San Félix,

1800-1856 m (14 USNM); CHIRIQUI: Cerro Punta (1 USNM); Cerro Punta, 6500 ft (1 USNM - holotype of C. zeteki); Cerro Punta, 2700 ft (2 USNM); Cerro Punta, Boquete Trail, 6800 ft (1 USNM); 24 km NNE of San Félix, 1275-1350 m (6 USNM); 24.5 km NNE of San Félix, 1325-1350 m (2 USNM); 14.5 km NW of El Volcán, Finca Santa Clara, 8°51'30"N, 82°44'45"W, 1200-2150 m (12 USNM); Santa Clara, Volcán de Chiriquí, 1700 m (3 USNM); Santa Clara, on the Pan American road 15 mi from Costa Rica, 4200 ft (1 AMNH - holotype of C. tersus).

FOSSIL *CRYPTOTIS* (INSECTIVORA: SORICIDAE) FROM THE PLEISTOCENE OF THE YUCATAN PENINSULA, MEXICO

Modern small-eared shrews of the genus *Cryptotis* are found from southern Ontario, across much of the eastern and midwestern United States, through portions of Mexico and Central America, and in the northern Andean highlands. Despite their wide distribution, most members of the genus are poorly known, and they are relatively uncommon in systematic collections due to their small size and difficulty of capture using conventional traps. Only three species of *Cryptotis* have been reported as Quaternary fossils: *C. parva*, one of the most widespread modern taxa, is known from at least 21 sites in the United States (Lundelius et al., 1983); *C. mexicanus* has been reported from San Josecito Cave, Nuevo Leon, Mexico (Findley, 1953); and *C. mayensis* has been reported from Loltun and Actun Spukil, Yucatan, Mexico (Hatt, 1953b; Alvarez, 1982). Fossils identified as *C. mayensis* are of particular interest because modern members of this species have a limited distribution in the harsh, seasonally dry environment of the Yucatan Peninsula, which is uninhabited by any other soricid. Most Mexican and Central American species of *Cryptotis* occur at elevations above 500 m, and many are

restricted to highlands above 1000 m. Cryptotis mayensis is the only species in the genus restricted to lowland environments below 100 m.

Hatt (1953a, b) carried out excavations in nine caves during expeditions to Yucatan in 1929 and 1947. In a remote portion of of one cave, Actun Spukil (Mayan for "Cave of Mice"), Hatt (1953b) recovered remains of a diverse Pleistocene vertebrate fauna. Among this material were mandibles of small-eared shrews, which were referred by Hatt (1953b) to C. mayensis.

A partial mandible of C. mayensis also was reported from Pleistocene sediments in the cave of Loltún (Alvarez, 1982), and additional material has since been identified from that site (J. Arroyo C., in lit.). Unfortunately, I have not yet had the opportunity to inspect this material.

As part of a comprehensive taxonomic study of Central American shrews of the genus Cryptotis (Woodman and Timm, 1992, submitted, manuscript), I studied fossil mandibles of shrews from Actul Spukil. It is the purpose of this paper to confirm the identity of the fossil Cryptotis recovered from Actun Spukil and to report on changes in the shrew fauna of the Yucatan since late Pleistocene time.

Locality

Actun Spukil is a subterranean solution cavern located approximately 4 km SSW of Calcehtok [or 6 km SE of the ruins of Oxkintok] on the southwestern serranía, western Yucatan, Mexico. Surface elevation is ca. 60 m. Actun Spukil consists of a long corridor connecting two large sinkholes and at least one other large, subterranean room. The cave is described in detail by Mercer (1896) and Hatt (1953a).

Pleistocene fossil remains, including Cryptotis, were recovered from a deposit of unconsolidated, "soft, red earth" in a small room of difficult access in the lowest reaches of the cave, approximately 50 m below the ground surface (Hatt, 1953a). These sediments may be roughly equivalent in age to Pleistocene red earth deposits reported by Alvarez (1982) from Loltún. Hatt carried out excavations in this chamber of the cave in 1929 (Hatt's Lot 15) and again in 1947 (Lots 30-34). All Cryptotis remains from the chamber are from Lot 15 (= AMNH 212645). Hatt (1953a) speculated that remains in the lower chamber sediments may have been of animals which accidentally fell into the vertical openings or which were brought into Actun Spukil by owls; the bones subsequently washed down into the lower chamber from above. Owl still roosted in the cave at the time of

Hatt's excavations there, and owl pellets were collected by him (Hatt, 1953a - Lot 16) in 1929 from the first large chamber (Rotunda I) beneath the main entrance to Actun Spukil.

At the time of the first excavations in 1929, it appeared that approximately 4.5 m of the upper layers of the deposit previously had been removed by local inhabitants, perhaps for making pottery or for use as a building material (Hatt, 1953a). No human remains or artifacts were encountered in this deposit. Cultural remains in the lowest chamber were limited to the surface, and probably were associated with individuals mining the cave earth or seeking water in the cave (Hatt, 1953a).

Methods

Comparisons were made among the 16 fossil mandibles (9 right, 7 left) from Actun Spukil and mandibles of modern specimens of 16 C. mayensis (including 7 left dentaries from modern owl pellets collected in Actun Spukil), 11 C. merriami, and 13 mandibles (including 7 right dentaries) from owl pellets found in Cañon del Zopilote, Guerrero, which have been referred to C. mayensis, and may represent a population of that species outside of the Yucatan Peninsula (Woodman and Timm, manuscript). Both C. mayensis and C. merriami

previously were considered to be subspecies of C. nigrescens (Choate, 1970; Hall, 1981), but recently were shown to be distinct species (Woodman and Timm, manuscript). Cryptotis mayensis from Guerrero are similar morphologically, particularly in the structure of the mandible, to C. mayensis from the Yucatan Peninsula. Choate (1970) noted this close similarity in morphology, but suggested that the specimens from Guerrero could represent a separate subspecies of C. nigrescens because of the distance (> 950 km) and extensive biogeographical barriers between Cañon del Zopilote and the Yucatan Peninsula. Based on their distinct ecological and geographical distributions, the population in Guerrero and C. mayensis from the Yucatan may be separate species, but complete material of the Guerrero population is lacking, making extensive comparisons difficult (Woodman and Timm, manuscript).

All measurements reported herein are in millimeters. Measurements were taken to the nearest 0.1 mm using an ocular micrometer in a binocular microscope (Cryptotis) or a hand-held dial caliper (Ototylomys). Measurements from mandibles of Cryptotis include (Fig. 39): length from inferior sigmoid notch to mental foramen (lma); length from articular process to mental foramen (lmb); height of coronoid process (hcp); breadth of coronoid

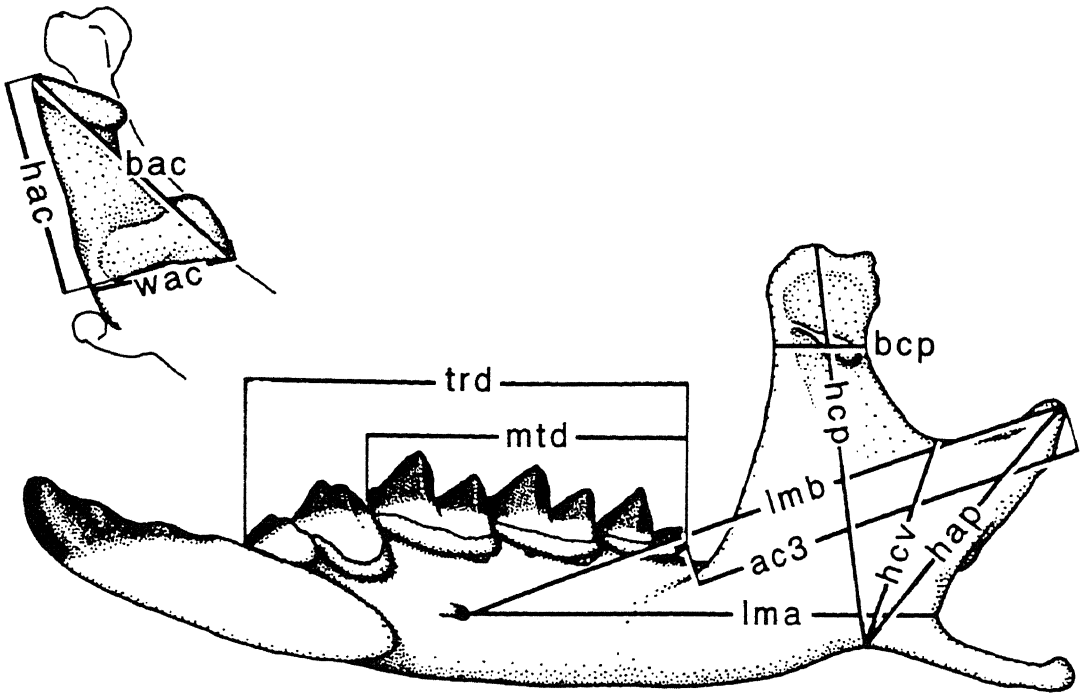

Figure 39. Mandibular measurements of Cryptotis used in this study. See text for explanation of abbreviations.

process (bcp); height of coronoid valley (hcv); height of articular process (hap); articular condyle to posterior edge of m3 (ac3); length of lower toothrow (trd); length of lower molar toothrow (mtd); height of articular condyle (hac), width of articular condyle (wac); breadth of articular condyle (bac).

Only complete, right mandibles of fossil (n = 5) and modern Cryptotis (only left mandibles from Actun Spukil owl roost) were used in statistical analyses. Analyses of variance (ANOVA) and principal components analysis (PCA) were carried out using BMDP on the University of Kansas Academic Computing Services' IBM VM/CMS computer system.

Differences between fossil specimens and modern C. mayensis from the Yucatan Peninsula first were tested by carrying out an ANOVA on each of nine variables (lma, lmb, hcp, bcp, hcv, hap, mtd, ac3, bac). Statistical significance was determined using Welch's test for equality of means, which does not assume equality of variances.

PCAs were carried out using the same nine variables to determine if specimens of Cryptotis would cluster in their a priori groupings when treated as a single population. The first PCA was carried out on the fossil specimens and 16 C. mayensis from the Yucatan Peninsula.

Two additional PCAs were run, one using the fossils, C. mayensis, and 7 Cryptotis from Guerrero; a third was used to describe the fossils, C. mayensis, specimens from Guerrero, and 11 C. merriami.

Specimens from the following institutions were used in his study: American Museum of Natural History, New York (AMNH); Angelo State University Natural History Collections, San Angelo (ASNHC); Instituto de Biología, Universidad Nacional Autónoma de Mexico, Mexico, D.F. (IBUNAM); University of Kansas Museum of Natural History, Lawrence (KU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Royal Ontario Museum, Toronto (ROM); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Universidad Nacional Autónoma de Honduras, Tegucigalpa (UNAH).

Associated Fauna and Age of Sediments

A list of the Pleistocene mammal fauna recovered from the lower chamber in Actun Spukil is presented in Table 8. Among the remains were a tympanic ring and a tooth fragment of a Pleistocene ground sloth, identified by Hatt (1953b) as ?Paramylodon. Paramylodon now is considered a junior synonym of Glossotherium (Engelmann, 1985), which has a terminal date in North America of 9,880 yrs B.P. at Hornsby Springs, Florida, and in South America of 11,040 yrs B.P. at Arroio Touro Passo, Brazil

Table 8. Mammal fauna from Actun Spukil reported by Hatt (1953b).

Pleistocene fauna (Lots 15, 30-34)	Modern Owl Roost (Lot 16)
Marsupialia	
Didelphis marsupialis (1)	*Marmosa canescens*
Marmosa canescens	
Insectivora	
Cryptotis mayensis	*Cryptotis mayensis*
Chiroptera	
Pteronotus parnellii	*Artibeus jamaicensis*
Mormoops megalophylla	*Mimon cozumelae*
Artibeus jamaicensis	
Mimon cozumelae	
Eptesicus furinalis	
Xenarthra	
cf. *Glossotherium*	
Lagomorpha	
Sylvilagus	*Sylvilagus*
Rodentia	
Oryzomys couesi	*Oligoryzomys fulvescens*
Otonyctomys hatti	*Ototylomys phyllotis*
Ototylomys phyllotis	*Peromyscus yucatanicus*
Peromyscus yucatanicus	*Sigmodon hispidus*
Reithrodontomys sp. (2)	*Heteromys gaumeri* (3)
Sigmodon hispidus	*Mus musculus*
Tylomys nudicaudatus	
Heteromys gaumeri (3)	
Sciurus yucatanensis	
Carnivora	
cf. *Urocyon cinereoargenteus*	
Felis pardalis	
Mephitis/Conepatus	
Mustela frenata	
Spilogale angustifrons	
Procyon lotor	
Artiodactyla	
Tayassu tajacu	

(1) These may be a mixture of *D. marsupialis* and *D. virginiana*.
(2) *Reithrodontomys gracilis* is the only species of harvest mouse currently known from the Yucatan Peninsula.
(3) These may include *H. desmarestianus* and *H. gaumeri*.

(Anderson, 1984). The deposit in which the ground sloth remains were found lacked cultural material and is probably at least 9,500 yrs old.

Several lines of evidence support a late Pleistocene date for the Actun Spukil fauna. In the deposit with Glossotherium were remains of climbing rats, Tylomys nudicaudatus (Hatt, 1953a, b), and highland wood-partridge, Dendrortyx leucophrys (Fisher, 1953), neither of which occurs on the Yucatan Peninsula today. The type material of an extinct xantusiid lizard, Lepidophyma arizeloglyphus (Langebartel, 1953) also was recovered from the cave sediments. An iguanid lizard, Ctenosauria premaxillaris, first recognized on the basis of remains from this site, now is considered a nomen dubium (Langebartel, 1953; Estes, 1983).

Hatt (1953a, b) reported remains of the big-eared climbing rat, Ototylomys, from the Pleistocene deposit in Actun Spukil as O. guatemalae, while those from the modern owl roost he identified as O. phyllotis. Ototylomys guatemalae has since been synonymized with O. phyllotis (Lawlor, 1969), but the fact that Hatt recognized the fossil and the modern Ototylomys as distinct taxa suggested that the two groups appeared different to him. Comparison of measurements of the fossils recorded by Hatt (1953b:66) with 35 modern

specimens of O. phyllotis collected from the Mexican states of Campeche, Quintana Roo, and Yucatan shows the fossils to average distinctly larger than modern specimens for each variable (Table 9). This difference in size has also been show for Pleistocene O. phyllotis from Loltún (Alvarez, 1982).

Proportions of certain species of rodents are notably different in the late Pleistocene sample from Actun Spukil than they are in the sample from the modern owl roost in the same cave. In a comparison of total numbers of mandibles of the rodent genera Heteromys, Oryzomys, Otonyctomys, Ototylomys, and Sigmodon recovered from the two samples, Sigmodon makes up nearly 50% of the mandibles in the fossil deposit, whereas Heteromys dominates in the modern owl pellets (Table 10; Hatt, 1953b). Evidence presented by Alvarez (1982) indicates that dominance of Sigmodon may characterize certain phases of the Pleistocene environment of the Yucatan Peninsula (Alvarez, 1982).

The endemic Yucatan vesper mouse, Otonyctomys hatti, appears to have been common in the Pleistocene environment near the cave, but it is not known there today (Table 10), and it is considered relatively rare throughout the Yucatan Peninsula because of its scarcity in systematic collections. Peterson's (1966) record of

Table 9. Cranial measurements of Pleistocene Ototylomys from Actun Spukil reported by Hatt (1953b:66) compared with those of modern specimens from Campeche, Quintana Roo, and Yucatan. Statistics presented are mean (specimens from Actun Spukil) or mean ± standard deviation (modern specimens) and range, with sample size in parentheses.

	Actun Spukil	modern specimens
length of maxillary toothrow		
	6.7 6.5 - 7.0 (7)	5.8 ± 0.2 5.5 - 6.3 (35)
width of M^1		
	1.9 1.8 - 1.9 (7)	1.6 ± 0.1 1.4 - 1.8 (35)
length of palate		
	5.4 - 5.8 (2)	4.7 ± 0.3 4.2 - 5.2 (35)
width across M^1s		
	6.5 - 6.8 (2)	5.9 ± 0.3 5.4 - 6.8 (35)
width of zygomatic plate		
	4.3 4.1 - 4.5 (3)	3.3 ± 0.2 2.9 - 3.8 (35)
length of mandible		
	22.1 21.0 - 23.0 (4)	21.3 ± 1.0 19.5 - 23.4 (35)
length of lower molar row		
	6.7 6.4 - 7.1 (20)	5.9 ± 0.2 5.4 - 6.3 (35)

Table 10. Total numbers of mandibles of Heteromys, Oryzomys, Ototylomys, Sigmodon, and Otonyctomys recovered from Pleistocene sediments and from modern owl pellets in Actun Spukil (Hatt, 1953b). Relative percentages are given in parentheses.

	Pleistocene	Modern
Heteromys	7 (3)	127 (84)
Oryzomys couesi	1 (<1)	0
O. fulvescens	0	2 (1)
Otonyctomys	18 (9)	0
Ototylomys	84 (42)	10 (6.5)
Sigmodon	91 (45)	13 (8.5)
Total	201	152

O. hatti from Actun Spukil, subsequently used by Hall (1981), is based on the Pleistocene specimens reported by Hatt (1953a, b).

Results

Mandibles of the fossils, modern C. mayensis from the Yucatan Peninula, specimens from Guerrero, and C. merriami all have similar dental characteristics. However, mandibles of C. merriami are distinguished from the others by being relatively longer and having a coronoid process that is lower, narrower, and less broadly rounded. Also, the external temporal fossa and coronoid spicule often are not as well developed in C. merriami as they are on mandibles of the fossils from Actun Spukil, the Guerrero specimens, or modern C. mayensis.

The fossil mandibles, C. mayensis from the Yucatan, and the specimens from Guerrero are very similar in overall appearance, and they are difficult to distinguish. However, the Pleistocene fossils differ from modern C. mayensis in having a wider mean coronoid process (bcp: $F = 14.21$, $P = 0.0044$) and narrower mean articular condyles (bac: $F = 14.81$, $P = 0.0049$). The two variables mtd ($F = 4.53$, $P = 0.0623$) and hcv ($F = 3.31$, $P = 0.1286$) could not be shown to be significantly different, but their values were close to being

significant. Means of all other variables were similar ($P < 0.30$) for the two groups.

In the PCAs the fossils generally grouped together and were often separable from the other two groups. In the plot of factor 1 vs. factor 2 from the PCA using fossil mandibles and C. mayensis (Fig. 40), the fossils separate out on factor 2. All variables weighed out heavily on factor 1, indicating that it represents overall size of the specimens, and factor 2 is a contrast between a combination of bcp and bac vs. a negatively weighted combination of ml and hcv. In addition to narrower coronoid processes and articular condyles, the fossils tend to have longer mandibles and shallower coronoid valleys than C. mayensis.

The plot of scores from the PCA using three groups (fossils, C. mayensis, and specimens from Guerrero) again shows the fossils tending to cluster at one extreme of factor 2 (Fig. 41). In this analysis factor 2 is a contrast between mtr and a negatively weighted combination of bcp and bac. The fossils have relatively longer lower molar toothrows and narrower coronoid processes and articular condyles than either C. mayensis or Cryptotis from Guerrero. Mandibles of C. mayensis and specimens from Guerrero are indistinguishable from each other on any axes.

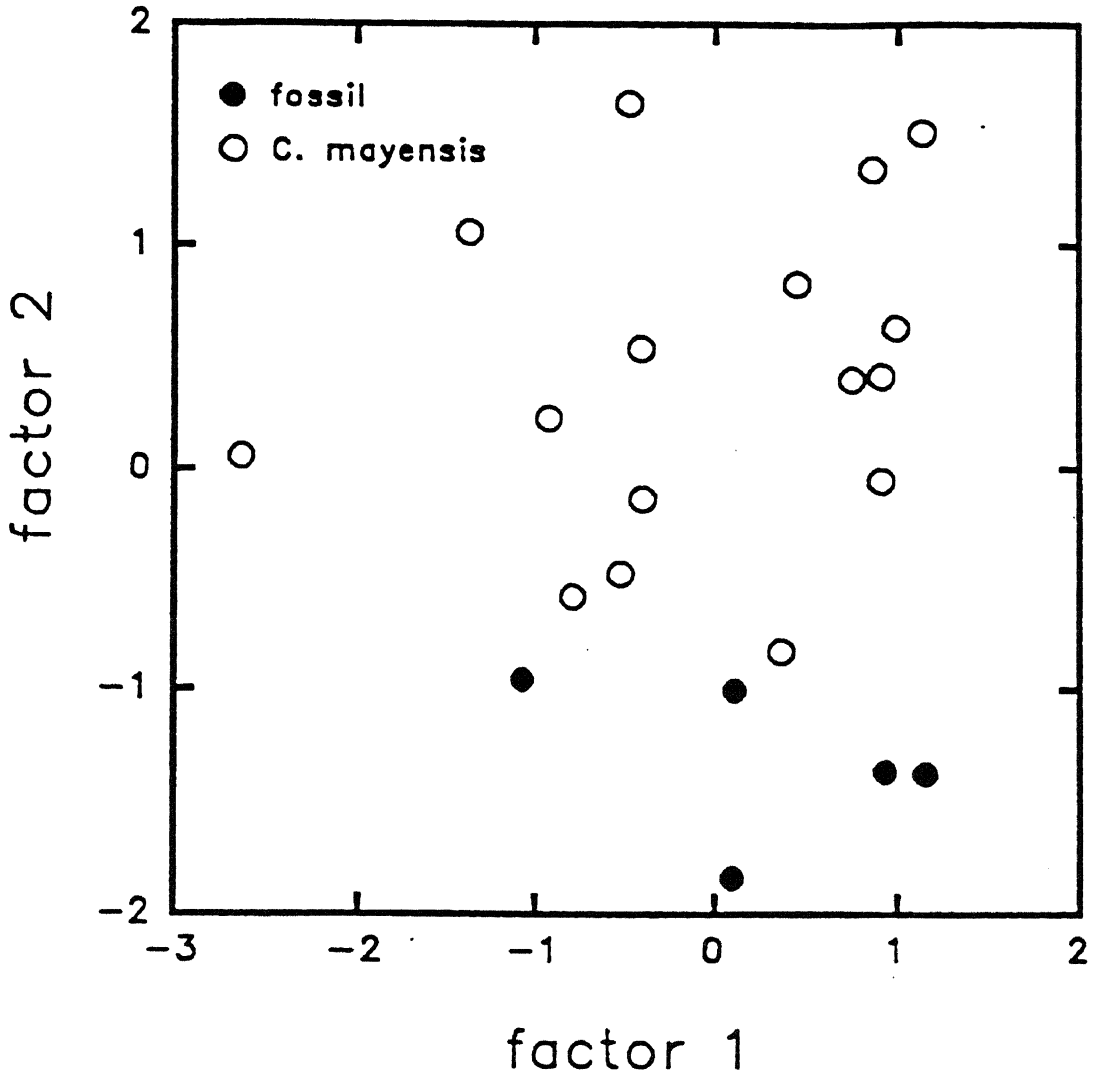

Figure 40. Plot of specimens of fossil Cryptotis from Actun Spukil and modern C. mayensis on principal components factor axes 1 and 2.

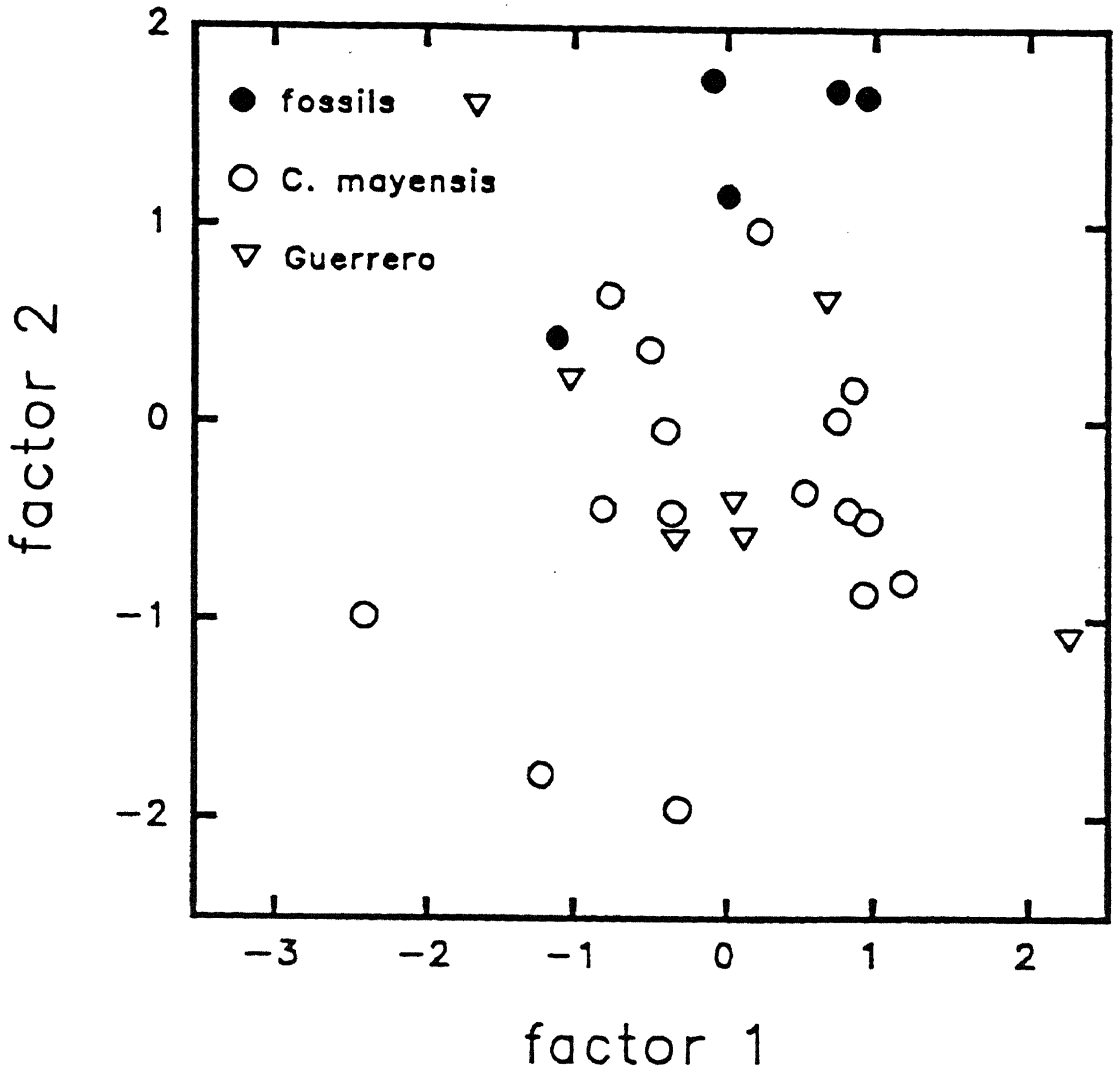

Figure 41. Plot of fossils, C. mayensis, and Cryptotis from Guerrero on principal components factor axes 1 and 2.

The plot of scores from the PCA of the fossils, C. mayensis, C. merriami, and the the Guerrero specimens shows a clear separation of C. mayensis and C. merriami on a combination of factors 1 and 2 (Fig. 42), but this separation primarily is due to the influence of factor 2. Specimens from Guerrero again are indistinguishable from C. mayensis, and the fossils are clustered in an area where they overlap both C. mayensis and C. merriami. Factor 2 in this analysis represents a contrast between a combination of mtr and ml vs. a negatively weighted bcp. Cryptotis merriami tend to have longer mandibles and concurrently longer toothrows than C. mayensis, and they have narrower coronoid processes. The fossils are intermediate between the two groups. In a plot of factor 2 against factor 3 there is again a separation between C. mayensis and C. merriami (Fig. 43). The fossils plot together toward one end of axis 3, where they still overlap with both C. mayensis and C. merriami, but to a lesser extent. Factor 3 is a contrast between hcv and a negatively weighted bac. The fossils tend to have shallower coronoid valleys and narrower articular condyles than any of the other three groups.

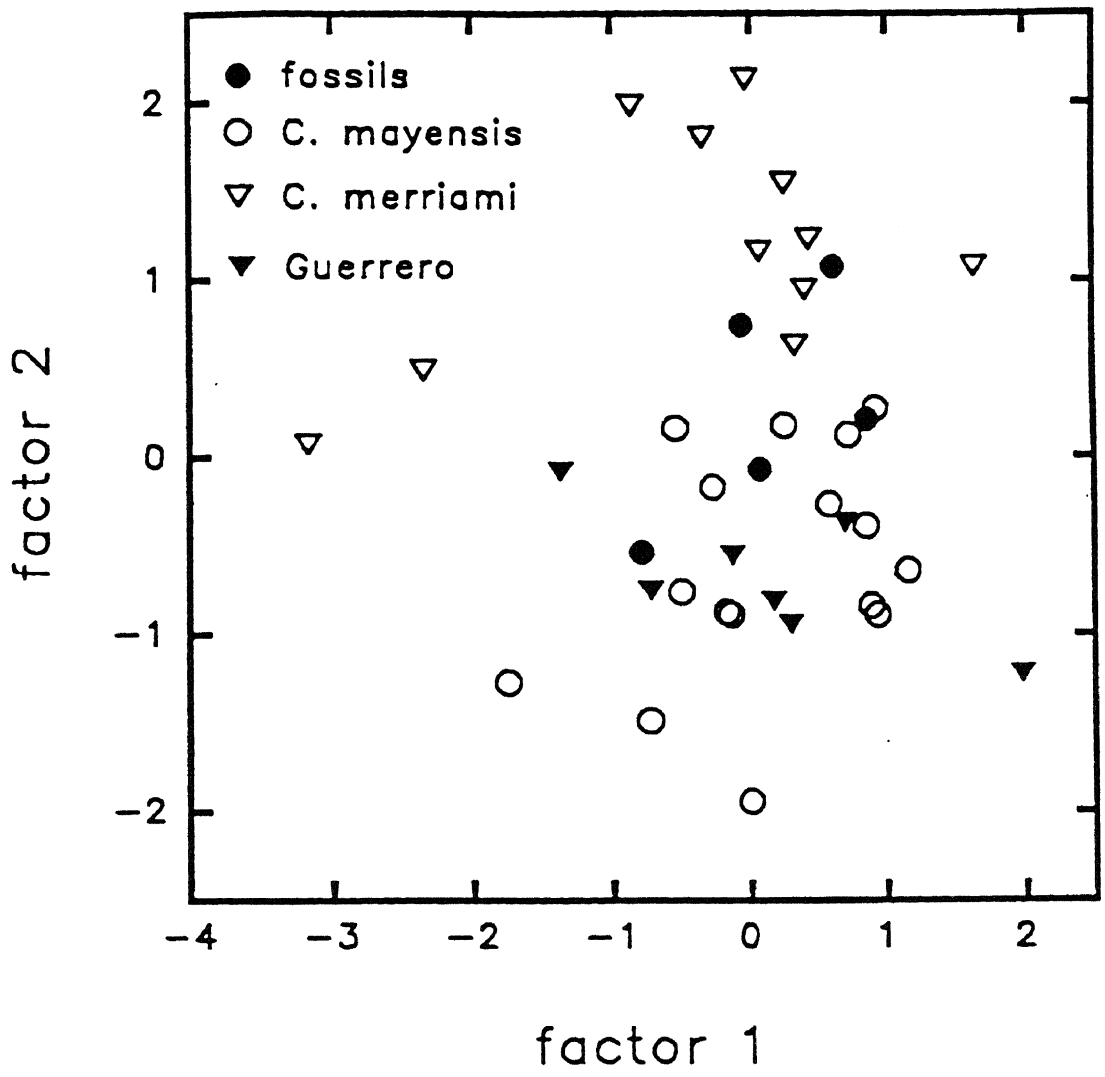

Figure 42. Plot of fossils, C. mayensis, Cryptotis from Guerrero, and C. merriami on principal components factor axes 1 and 2.

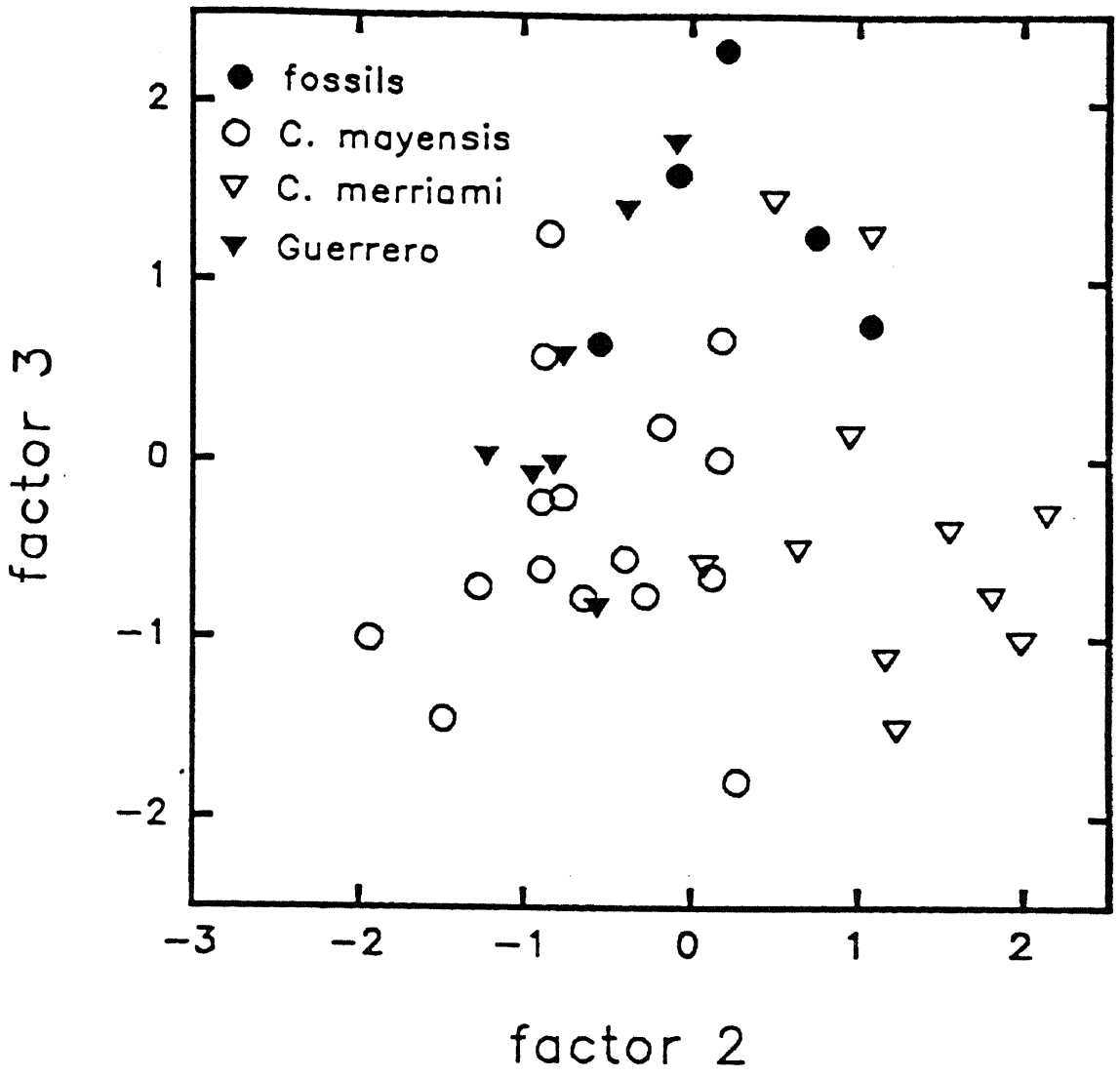

Figure 43. Plot of fossils, C. mayensis, Cryptotis from Guerrero, and C. merriami on principal components factor axes 2 and 3.

Discussion

The fossil shrew mandibles from Actun Spukil clearly are different in relative proportions from modern C. mayensis from the Yucatan and from Guerrero. The Pleistocene fossils in some respects appear intermediate between C. mayensis and C. merriami as described by PCA (Fig. 42). However, as described above, mandibles of C. merriami differ morphologically from those of the fossils and modern C. mayensis. The fossils from Actun Spukil most likely represent a former population of C. mayensis that differed from modern C. mayensis in certain mean morphological proportions, but was otherwise the same animal. No taxonomic change is warranted.

Changes in size and/or proportions between among Pleistocene populations, or late Pleistocene and Holocene populations, of a species are known to have occurred in many species of mammals (Guthrie, 1984) and generally are correlated with shifts in climatic conditions between glacial and interglacial epochs (Nelson and Semken, 1970). Morphometric changes within mammal species are especially well documented for the last major shift between 12,000 and 10,000 yr B.P. that resulted in biotic reorganization of communities as animal and plant species responded individually to new

climatic conditions (Graham and Lundelius, 1984) and, in some regions, reduced growing season (Guthrie, 1984).

Evidence from studies of mammals (Hatt, 1953b; Alvarez, 1982; Arroyo C. and Alvarez, 1990) and molluscs (Polaco, 1982) suggests that late Pleistocene and early Holocene environments of the Yucatan fluctuated, at least locally, between tropical deciduous forest and more open vegetation representative of drier conditions, such as thorn forest, meadow, or grassland. Alvarez (1982) recognized four climatic phases represented in the sediments at Loltún based on relative frequencies of remains of the rodents Heteromys, Oryzomys, Ototylomys, and Sigmodon. High percentages of Sigmodon and proportionally low numbers of Heteromys in the latest Pleistocene suggest that open vegetation dominated. Arroyo and Alvarez (1990) interpreted the bat fauna from Loltún to show a dominance of open vegetation in the Late Pleistocene up through the time of the Pleistocene/Holocene transition. The presence of open vegetation is supported further by the presence of horse (Equus) and camel (Tanupolama) remains at Loltún (Alvarez, 1982), and at Actun Spukil by the dominance of Sigmodon in the rodent fauna (Table 10; Hatt, 1953b), and by the presence of Glossotherium, which is believed to have inhabited open country (Anderson, 1984).

In contrast, several animals in the fauna from Actun Spukil suggest that late Pleistocene conditions were not as seasonally severe as they are today. Tylomys nudicaudatus is an arboreal rat considered typical of moist, closed-canopy forests. It does not occur on the Yucatan Peninsula today, but is found in adjacent, more mesic Chiapas, Guatemala, and southern Belize.

Modern Ototylomys phyllotis from the Yucatan Peninsula average among the smallest of the species, and there are clinal trends of increasing size to the south and southeast, and to the northwest. Size also tends to increase with altitude (Lawlor, 1969). Remains of O. phyllotis from Pleistocene sediments of Actun Spukil and Loltún (Alvarez, 1982) are most similar in size to modern specimens reported from the highlands of Guatemala (Lawlor, 1969).

Remains of highland wood-partridge, Dendrortyx leucophrys, in Actun Spukil indicate its presence in the Pleistocene fauna of the Yucatan Peninsula. Today, it occurs in foothills and highlands of Chiapas and Guatemala south to Costa Rica, but does not range into the lowlands of the Yucatan Peninsula. Wood-partridges inhabit secondary growth and brushy understory in montane forest and cloud forest (Land, 1970).

Late Pleistocene mammal faunas from temperate North

America are typified by higher diversities than occur at the same localities today (Graham, 1976). This diversity is not simply because of the inclusion of now extinct species, but also is a reflection of the cooccurrence of extant species which currently are allopatric and are thought to be ecologically incompatible in modern environments (Graham, 1976; Graham and Lundelius, 1984).

The inclusion of both extant and extirpated species in the late Pleistocene fauna from Actun Spukil suggests a more moderate environment at that time. The presence of these animals together suggests less seasonally extreme temperatures in the Yucatan during the late Pleistocene.

It is likely that the proportional differences seen between late Pleistocene and modern C. mayensis from the Yucatan Peninsula may have been a response to the change from more moderate to more severe conditions at the end of the Pleistocene. The convergence in general shape of Pleistocene C. mayensis toward modern C. merriami may have been a response to aspects of an environment somewhat more similar to that occupied today by C. merriami in the highlands of central Guatemala.

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Specimens Examined

Cryptotis fossils (16).--**MEXICO:** YUCATAN: Actun Spukil, excavations (16 AMNH).

C. mayensis (18).--**BELIZE:** CAYO DISTRICT: Baking Pot (1 ROM); **MEXICO:** CAMPECHE: 60 km SE of Dzibalchen (19°10'N, 89°20'W) (1 ROM, 1 ASNHC); 7.5 km W of Escárcega (1 ASNHC); QUINTANA ROO: 6 km S, 1.5 km W of Tres Garantías (1 ASNHC); YUCATAN: Actun Spukil, owl perch (9 AMNH); Loltún (2 ASNHC); 6 km S Mérida (1 KU); 13 km W Peto (1 KU).

Cryptotis c.f. mayensis" (13).--**MEXICO:** GUERRERO: Zumpango del Río District, Cañon del Zopilote, 11.5 km S of the Río Mescala bridge near Mescala; Cueva de Macuiltzingo (13 IBUNAM).

C. merriami (11).--**EL SALVADOR:** MORAZAN: Mt. Cacaguatique, north slope, 3800-4000 ft (1 MVZ); SAN MIGUEL: Mt. Cacaguatique, 3500-4000 ft (4 MVZ; 2 UMMZ); **GUATEMALA:** ALTA VERAPAZ: Tucurú, Hacienda Concepción,

1100 m (1 UMMZ); HUEHUETENANGO: Barillas, Hacienda Santa Gregoria (1 UMMZ); **HONDURAS:** FRANCISCO MORAZAN: La Tigre National Park, San Juancito, La Rosario (1 UNAH); **NICARAGUA:** MATAGALPA: Santa Maria de Ostuma (1 UMMZ).

Otonyctomys hatti (35).--**MEXICO:** CAMPECHE: 5 km S Champotón, 10 m (2 KU); 7.5 km W Escarcega, 65 m (2 KU); 65 km S, 128 km E Escarcega (2 KU); 103 km SE Escarcega (1 KU); QUINTANA ROO: Pueblo Nuevo X-Can, 10 m (3 KU); 2 km S Pueblo Nuevo X-Can, 10 m (1 KU); 4 km NNE Felipe Carrillo Puerto (6 KU); 60 km N, 16 km E Chetumal (2 KU); 83 km W Chetumal (1 KU); YUCATAN: 3 km N Pisté (4 KU); Pisté, 10 m (1 KU); Cenote Seco, 2 km E Chichén Itzá (2 KU); Chichén Itzá, 10 m (1 KU); 6 km N Tizimin (1 KU); 66 km NE Mérida (4 KU); Valladolid (1 KU).

EVOLUTIONARY RELATIONSHIPS AMONG THE SMALL-EARED SHREWS OF THE GENUS CRYPTOTIS (INSECTIVORA: SORICIDAE)

Small-eared shrews of the New World genus Cryptotis occur from southernmost Canada, through the eastern half of the United States, parts of Mexico and Central America, to the northern Andean Highlands of South America. Relationships of this genus within the Soricidae are fairly well established (Repenning, 1967; George, 1986). The sister group of Cryptotis is Blarina, a genus in which Cryptotis for a long time was treated as a subgenus (e.g., Merriam, 1895). Cryptotis and Blarina form the tribe Blarinini, which has a sister group relationship with Sorex, the sole modern genus in the Soricini (Fig. 44). The next outgroup is the Neomyini, including Megasorex, Neomys, and Notiosorex, among others. These three tribes together form the subfamily Soricinae (Repenning, 1967; George, 1986), one of the two subfamilies in the Soricidae.

Although higher level relationships among shrews are well substantiated, relationships within genera are poorly understood. This is particularly true for small-eared shrews of the genus Cryptotis, in which biological studies have been rare. Even the species-level diversity in this genus is poorly known. Prior to

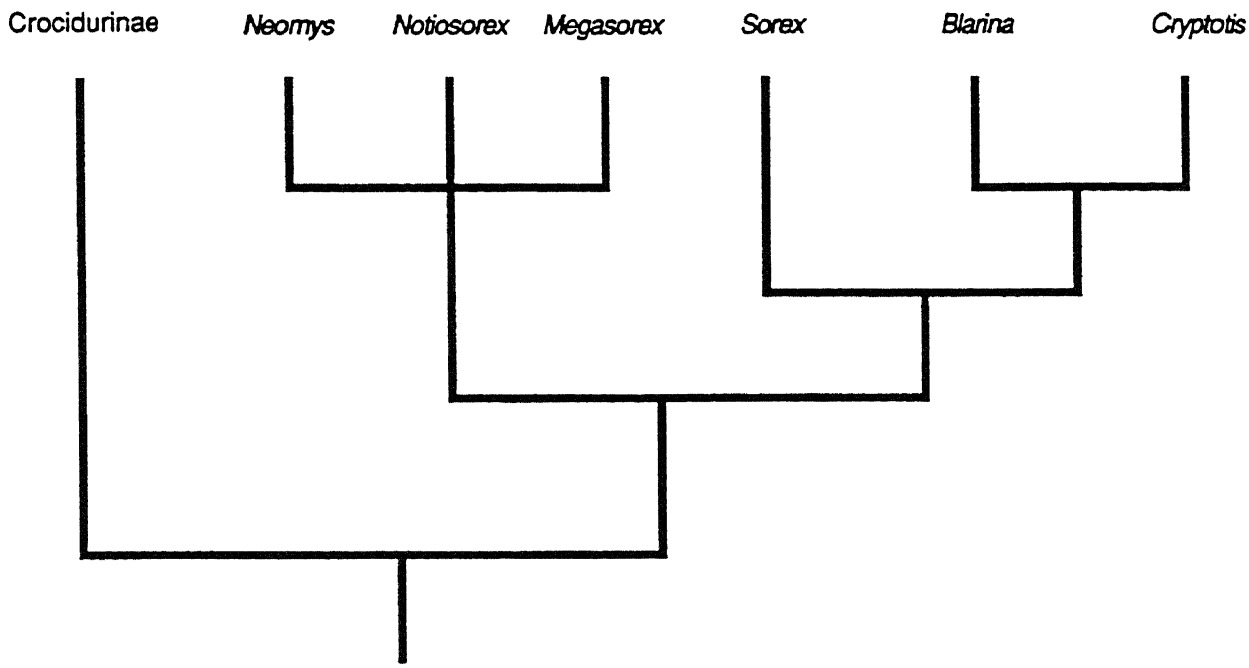

Figure 44. Relationships among the taxa used as outgroups to Cryptotis, based on Repenning (1967) and George (1986, 1988).

Choate's (1970) important review of Middle American species of Cryptotis, there were thought to be as many as 29 species (40 taxa, i.e., monotypic species plus subspecies) in the genus (Hall and Kelson, 1959; Cabrera, 1958), and there were no published phylogenies. Choate's (1970) investigations combined a large number of Mexican and Central American taxa and reduced the total number of species in the genus to 12 (28 taxa). His work has been followed for more than twenty years (Hall, 1981; Nowak, 1991). Choate (1970) also provided the first phylogeny of Cryptotis (Fig. 45). This phylogeny consists of a basal polytomy leading to four species groups: the C. parva group, consisting of C. nigrescens and C. parva; C. mexicana group, with C. goldmani, C. goodwini, and C. mexicana; C. thomasi group, made up of the South American species C. avia, C. montivaga, C. squamipes, and C. thomasi; and so-called "relict species", including C. endersi, C. gracilis, and C. magna. Also included were some fossil species and a fossil genus considered closely related to Cryptotis. Unfortunately, Choate did not map out character distributions used to support his phylogeny.

Recent collecting has increased samples sizes of many taxa of Cryptotis, permitting more intensive study of patterns of speciation, particularly in Mexico and

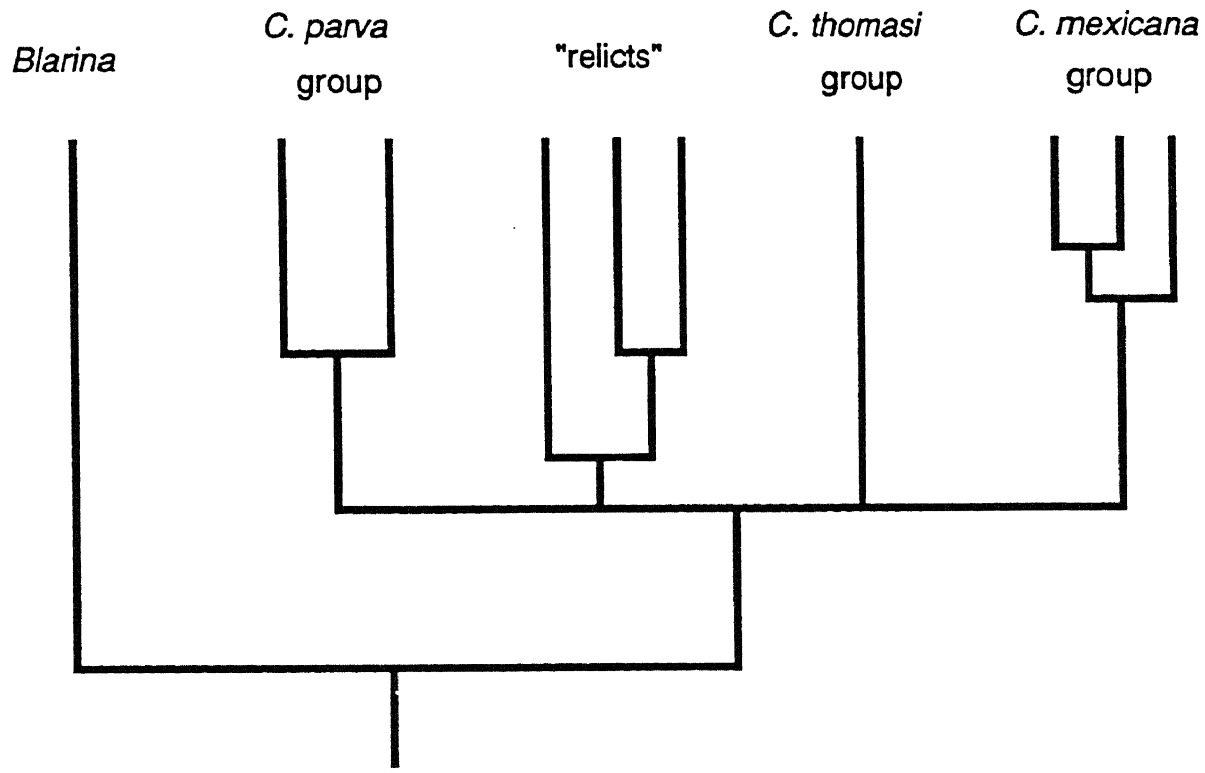

Figure 45. Phylogeny of Cryptotis proposed by Choate (1970).

Central America. This work has increased the known diversity of the genus by the description of new species and by permitting recognition of previously described taxa (e.g., subspecies) as valid species (Woodman and Timm, 1992; submitted; manuscript a; manuscript b). Currently 25 species (36 taxa) can be counted in the genus.

The purposes of this paper are (1) to test Choate's (1970) phylogeny of Cryptotis using an specific, expanded character set; (2) investigate the relationships of species not included in Choate's review; (3) propose a new hypothesis of relationships, if necessary; and (4) use the proposed phylogeny to revise the classification of the small-eared shrews.

Methodology

Transformation series are referred to below by the abbreviation TS, e.g., TS 4. Individual characters are designated by numbers within parentheses (e.g., (0), (1), etc.) within the context of their respective transformation series.

Data for this analysis were collected on 19 transformation series containing 44 characters. Multiple outgroup comparison was used to determine polarities of individual transformation series, and the most parsimonious explanation was sought in the

construction of trees (Wiley, 1981; Maddison et al., 1984), from which phylogenies were inferred.

Six genera of soricids were used as outgroups to independently polarize transformation series. Relationships among these six genera and their relationship with Cryptotis (Fig. 44) is based on craniodental morphology of fossil and modern soricine shrews (Repenning, 1967), and allozyme electrophoresis (George, 1986, 1988). Blarina was used as the sister group to Cryptotis. Characters were established for Blarina using three species in an unresolved trichotomy: B. brevicauda, B. carolinensis, and B. hylophaga. Three species of Sorex, each representing a distinct subgenus (George, 1988), were used to determine characters for the second outgroup: S. (Otisorex) haydeni, S. (Sorex) tundrensis, S. (unnamed subgenus) trowbridgii. For the third outgroup three neomyines were used in an unresolved trichotomy: Megasorex gigas, Notiosorex crawfordi, and Neomys fodiens. No crocidurines, the sister group to the soricines, were included in the analysis. Also, no fossil taxa were included, although five fossil genera have been placed in Blarinini by paleontologists: Blarinoides (Repenning, 1967; Rzebik-Kowalska, 1976), Mafia (Rzebik-Kowalska, 1990), Paracryptotis (Repenning, 1967; Choate, 1970),

Shikamainosorex (this may be congeneric with Paracryptotis - Repenning, 1967; Rzebik-Kowalska and Hasegawa, 1976), and Sulimskia (Rzebik-Kowalska, 1990). There are three described species of fossil Cryptotis, also not included in this analysis: C. adamsi, C. meadensis, and C. kansensis (Repenning, 1967; Choate, 1970). Inclusion/exclusion of fossil taxa may affect the determination of transformation series polarities at some ancestral nodes. However, the fossil material lacks information on external characters and is too fragmentary to get complete suites of craniodental characters.

A hypothetical ancestor was developed from the outgroups and polarities assigned to it using ACTRAN and DELTRAN optimization procedures as explained by Wiley et al. (1991) along the lineage from the Neomyini to the Blarinini. Where ACCTRAN and DELTRAN optimizations were in disagreement about the character for a specific transition series, the transition series was coded as polymorphic in the hypothetical ancestor. The hypothetical ancestor served as the outgroup for all analyses of Cryptotis.

All currently recognized species of Cryptotis were included in the analysis, with the exception of C. montivaga, for which insufficient specimens were

available. Most subspecies of C. mexicana and C. thomasi were considered together, although some of these may prove to be distinct species. However, C. mexicana peregrina, which is clearly differentiated from the other subspecies of C. mexicana on the structure of its forefeet and claws (TS 1 & 2), and C. thomasi equatoris, which differs from the other taxa included in C. thomasi in a number of characters, were included in the analysis as distinct taxa. The taxa I include in C. thomasi (medillinia, meridensis, thomasi) also exhibit some differences, but further analysis awaits a comprehensive revision of this group. It is very likely that the diversity of South American species is much larger than currently recognized. For the purposes of this analysis, all subspecies of C. parva were considered together. However, these taxa can be divided into northern and southern groups based on depth of the sigmoid notch (TS 10). I refer to the southern group of subspecies (orophila, pueblensis, tropicalis) as C. orophila and to northern subspecies (berlandieri, floridana, parva) as C. parva. Lack of data on C. parva soricina makes me uncomfortable in treating these divisions more formally at this time. This species group is in need of a comprehensive revision. In addition, the following groups of species were

represented in the analysis by a single taxon, because they shared the same characters for each transition series: C. mayensis and C. merriami (as C. mayensis); C. goodwini, C. griseoventris, and Cryptotis "C" (as C. goodwini); C. gracilis and C. jacksoni (as C. gracilis). The character matrix for all 42 taxa studied is presented in Table 11. The reduced character matrix (21 taxa) used for the phylogenetic analysis is presented in Table 12.

Cladograms were calculated using the computer program PAUP (release 3.0s, 1991) on an Apple Macintosh computer. Trees were constructed using a branch-and-bound branch addition algorithm employing furthest branch addition sequence. MAXTREES was set at 500.

All transformation series used in the analyses were equally weighted and treated as unordered, although I hypothesized that some transformation series would prove to be ordered. Strict and Adams consensus trees were calculated using all resulting, equally parsimonious trees.

Maddison (1991) showed that the complete set of most-parsimonious trees may include several distinct "islands" of minimum-length trees, which differ from each other in minor topological rearrangements. Heuristic tree-building algorithms routinely find such

Table 11. Complete character matrix for Cryptotis and each of its outgroups.

taxa	TS 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Neomys	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0
Notiosorex	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	2
Megasorex	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
S tundrensis	0	0	0	1	0	0	0	0	0	2	0	0	1	1	1	0	0	0	0
S haydeni	0	0	0	1	0	0	0	0	0	2	0	0	1	1	1	0	0	0	0
S trowbridgii	0	0	0	1	0	0	0	0	0	2	0	0	1	1	0	0	0	1	0
B brevicauda	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
B carolinensis	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
B hylophaga	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
parva	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	1	1	0	2
floridana	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	1	1	0	2
berlandieri	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	1	1	0	2
orophila	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	2
pueblensis	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	2
tropicalis	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	2
nigrescens	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	2
mayensis	0	0	1	0	1	0	0	1	0	0	1	0	0	0	1	0	1	1	2
merriami	0	0	1	0	1	0	0	1	0	0	1	0	0	0	1	0	1	1	2
hondurensis	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	2
mera	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	2
"D"	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	2
magna	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	1
mexicana	2	1	2	0	0	1	0	0	1	1	1	1	1	0	0	0	0	2	0
nelsoni	2	1	2	0	0	1	0	0	1	1	1	1	1	0	0	0	0	2	0
obscura	2	1	2	0	0	1	0	0	1	1	1	0	1	0	0	0	0	2	0
peregrina	1	0	2	0	0	1	0	0	1	1	1	1	1	0	0	0	0	2	0
alticola	3	1	2	0	0	1	0	0	1	1	0	0	1	0	0	1	1	2	2
goldmani	3	1	2	0	1	1	0	0	1	1	0	1	1	0	0	1	1	2	2
griseoventris	3	1	2	0	0	1	0	0	1	1	0	1	1	0	0	1	1	2	2
goodwini	3	1	2	0	0	1	0	0	1	1	0	1	1	0	0	1	1	2	2
"C"	3	1	2	0	0	1	0	0	1	1	0	1	1	0	0	1	1	2	2
gracilis	0	1	0	0	0	1	1	0	1	1	0	2	1	0	0	1	0	2	0
jacksoni	0	1	0	0	0	1	1	0	1	1	0	2	1	0	0	1	0	2	0
"A"	0	1	0	0	0	1	1	0	1	1	0	1	1	0	0	1	0	2	2
"B"	0	1	0	0	0	1	1	0	1	1	0	1	1	0	0	1	0	2	0
endersi	0	1	0	0	0	1	1	0	1	1	0	2	0	0	0	0	0	2	1
avia	0	1	0	0	0	1	1	0	1	0	0	1	1	0	0	1	0	2	2
squamipes	0	1	0	0	0	1	1	0	1	0	0	2	1	0	0	1	0	2	2
thomasi	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	2	2
equatoris	0	1	0	0	0	1	1	0	1	0	0	1	1	0	0	1	1	2	2
medellinia	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	2	1
meridensis	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	2	1

Table 12. Simplified character matrix for Cryptotis used to construct phylogeny.

taxa	TS 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
outgroup	0	0	0	0	0	0	0	/	0	0	/	0	0	0	0	0	/	0	0
parva	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	1	1	0	2
nigrescens	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	2
mayensis	0	0	1	0	1	0	0	1	0	0	1	0	0	0	1	0	1	1	2
hondurensis	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	2
mera	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	2
"D"	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	2
magna	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	1
mexicana	2	1	2	0	0	1	0	0	1	1	1	1	1	0	0	0	0	2	0
peregrina	1	0	2	0	0	1	0	0	1	1	1	1	1	0	0	0	0	2	0
alticola	3	1	2	0	0	1	0	0	1	1	0	0	1	0	0	1	1	2	2
goldmani	3	1	2	0	1	1	0	0	1	1	0	1	1	0	0	1	1	2	2
goodwini	3	1	2	0	0	1	0	0	1	1	0	1	1	0	0	1	1	2	2
gracilis	0	1	0	0	0	1	1	0	1	1	0	2	1	0	0	1	0	2	0
"A"	0	1	0	0	0	1	1	0	1	1	0	1	1	0	0	1	0	2	2
"B"	0	1	0	0	0	1	1	0	1	1	0	1	1	0	0	1	0	2	0
endersi	0	1	0	0	0	1	1	0	1	1	0	2	0	0	0	0	0	2	1
avia	0	1	0	0	0	1	1	0	1	0	0	1	1	0	0	1	0	2	2
squamipes	0	1	0	0	0	1	1	0	1	0	0	2	1	0	0	1	0	2	2
thomasi	0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	1	0	2	*
equatoris	0	1	0	0	0	1	1	0	1	0	0	1	1	0	0	1	1	2	2

/ - polymorphic (0/1); * - polymorphic (1/2)

islands, but a single search usually focuses on a single island, from which it can not leave because the islands are separated by areas of longer, non-minimum-length trees. Because it misses other islands, not all most-parsimonious trees are considered. Yet examination of all islands of trees is necessary because each island may have different implications for character evolution. Conducting multiple heuristic searches beginning with different starting points was suggested as one means of circumventing this problem (Maddison, 1991), and it should also avoid the problem of local optima. In order to test this and to determine the number of islands of minimum-length trees, the Cryptotis data matrix was input into a heuristic tree-building algorithm involving two steps: 1) random stepwise addition of taxa, holding 50 trees at each step, and 2) rearrangement of trees using tree-bisection-reconnection (TBR) branch-swapping. MAXTREES was set at 500. All minimum-length trees were saved (MULPARS). The heuristic program was run for 1000 replications.

Character Transformation Series

Forefeet and claws.

Enlargement of the forefeet and broadening of the foreclaws appear to occur together, and they have been

treated together as a single transformation series. I initially hypothesized that this was an ordered transformation series leading from (0) to (3). This is not supported by ACCTRAN or DELTRAN character optimizations on any of the minimum-length trees, however.

Elongation of the foreclaws does not keep pace with broadening, and elongation can occur without broadening, so this was considered as a separate transformation series (TS 2).

1. Forefeet: of normal size (0; Fig. 46A, B); slightly enlarged, with broad claws (1; Fig. 46C); enlarged, with broader claws (2; Fig. 46D); very much enlarged, with very broad claws (3; Fig. 46E). Polarized.

2. Foreclaws: of normal length (0; Fig. 46A, C); elongated (1; Fig. 46B, D, E). Polarized.

Position of zygomatic plate.

I follow Choate (1970) in use of the term "zygomatic plate" for the bridging structure distal to the infraorbital canal. This may seem somewhat inappropriate in as much as soricines lack a zygomatic arch, but it locates the structure in the correct region of the skull.

Position of the posterior border of the zygomatic

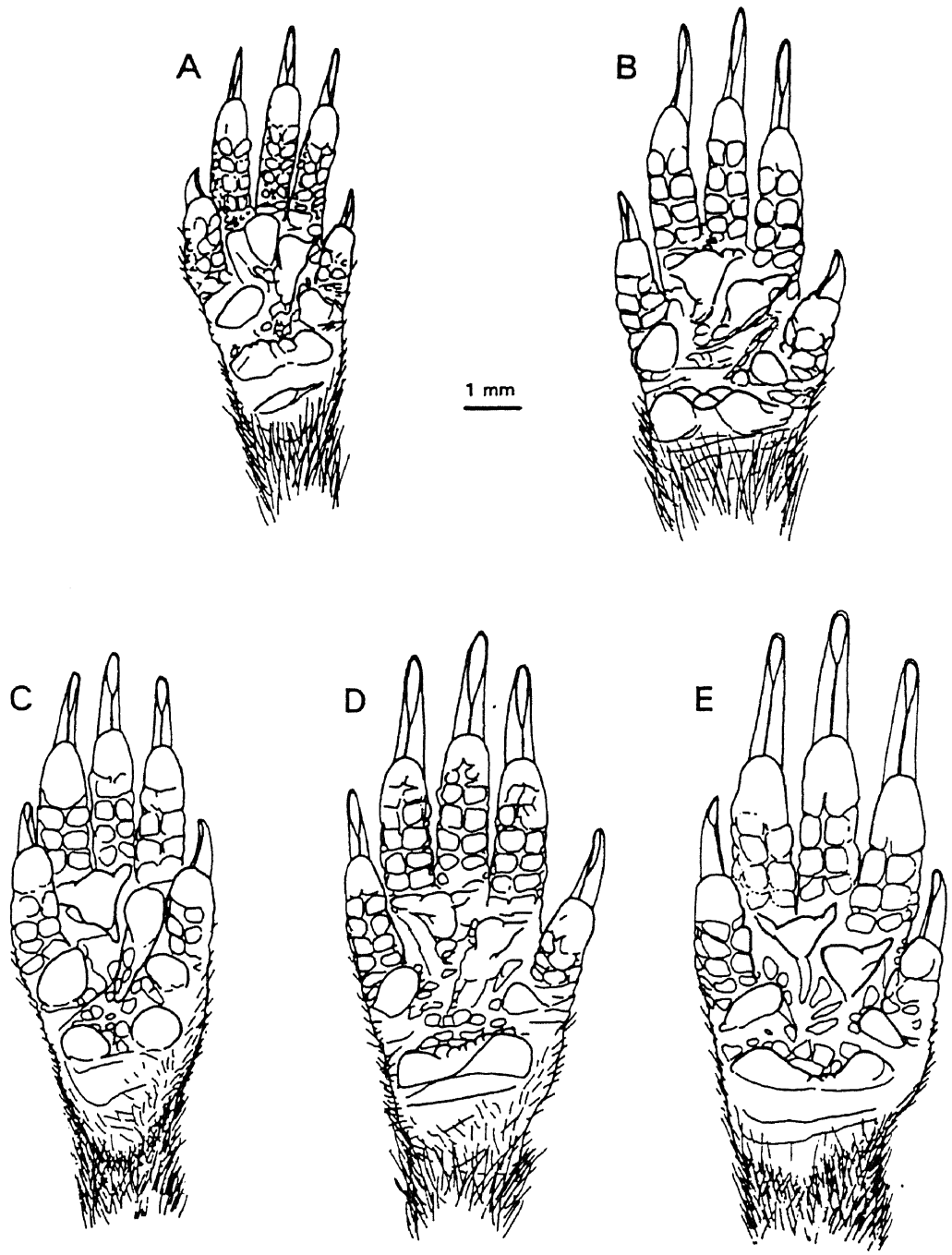

Figure 46. Dorsal view of right forefeet and foreclaws of Cryptotis parva orophila (A), C. jacksoni (B), C. mexicana peregrina (C), C. mexicana mexicana (D), and C. goldmani (E). All are from specimens of the same size (head and body length [HB] = 68 - 71 mm), except C. parva orophila (HB = 60 mm).

plate is treated as two separate transformation series because it was hypothesized that there are two contradictory apomorphic positions. Based on outgroup comparisons, the ancestral position of the zygomatic plate border is somewhat central (Fig. 47A). In some Cryptotis the posterior border of the zygomatic plate has shifted to a more posterior position (TS 3; Fig. 47B, C), while in C. parva the zygomatic plate is located more anteriorly (TS 4; Fig. 47D). This is complicated by the presence of an apomorphic condition in Sorex similar to that of C. parva, but character optimization indicates that this is a separate derivation of the character. It was assumed that the two apomorphic grades of posterior shifting of the plate (TS 3: (1), (2); Fig. 47B, C) represented two stages in a single, ordered transition series. However, this is not supported by character optimizations.

3. Position of posterior border of zygomatic plate: anterior to the posterior border of the maxillary process (0; Fig. 47A); even with the posterior border of the maxillary process, but separated from it by the posterior border of the palate (1; Fig. 47B); even with (or posterior to) and confluent with the posterior border of the maxillary process (2; Fig. 47C).

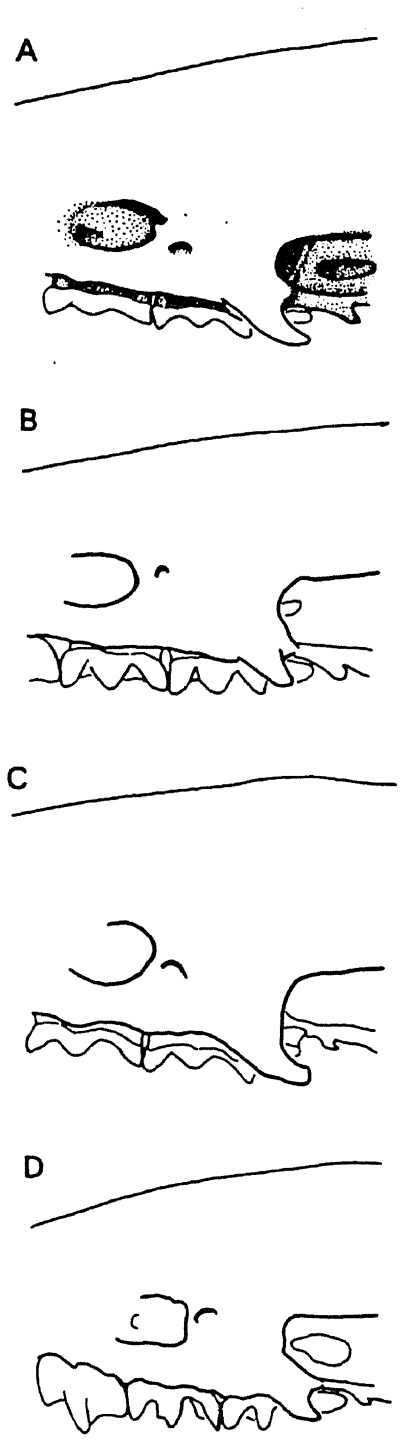

Figure 47. Lateral view of the left zygomatic plate of C. gracilis (A), C. mera (B), C. goldmani (C), and C. parva orophila (D).

Polarized.

4. Position of posterior border of zygomatic plate: posterior to the middle of the base of the maxillary process (0; Fig. 47A); anterior to the anterior border of the maxillary process (1; Fig. 47D). Polarized.

Foramen of ventral branch of sinus canal.

Cryptotis is unique among soricines in sometimes possessing a well-developed foramen posterior to the dorsal articular facet of the glenoid fossa (Fig. 24). A ventral extension of the sinus canal, which diverges from the main branch of the sinus canal just anterior to the cribiform plate, exits through this foramen. The foramen of the ventral branch of the sinus canal often is nearly the size of the anterior orifice of the sinus canal. Normally, a well-developed, bony canal is associated with the foramen, but occasionally the foramen leads directly to the braincase. Some species of Cryptotis possess a tiny foramen posterior to the dorsal articular facet, but normally it is not associated with a bony canal. Its presence in these species is highly variable, and these species never have a well-developed foramen. For these reasons, I code absence of a well-developed foramen of the ventral branch of the sinus canal the same, regardless of

whether a minute foramen is present.

5. Well-developed foramen of sinus canal: absent (1); present (2). Polarized.

Juncture of coronoid process with horizontal ramus.

The slope of the anterior edge of the coronoid process where it joins the horizontal ramus varies among species of Cryptotis from being nearly perpendicular to having a distinct posterior to anterior downward slope. The most nearly perpendicular, interpretted as plesiomorphic, occurs in Sorex and the Neomyini (Fig. 48A). A slightly lesser angle is seen in Blarina and in the Cryptotis parva and C. nigrescens species groups (Fig. 48B). Because a hypothetical ancestor was constructed from the outgroups, these two characters were combined to form character (0) used in the analysis. This prevents the hypothetical ancestor from being polymorphic and possibly misinterpreted in the computer analyses. The next lesser slope occurs in the C. mexicana group (Fig. 48C), and the lowest slope is seen in the C. gracilis group and the South American clade including C. thomasi (Fig. 48D). The last two characters were combined as character (1) because of difficulty in interpretting the C. goldmani/goodwini species group, in which both morphologies appear to be

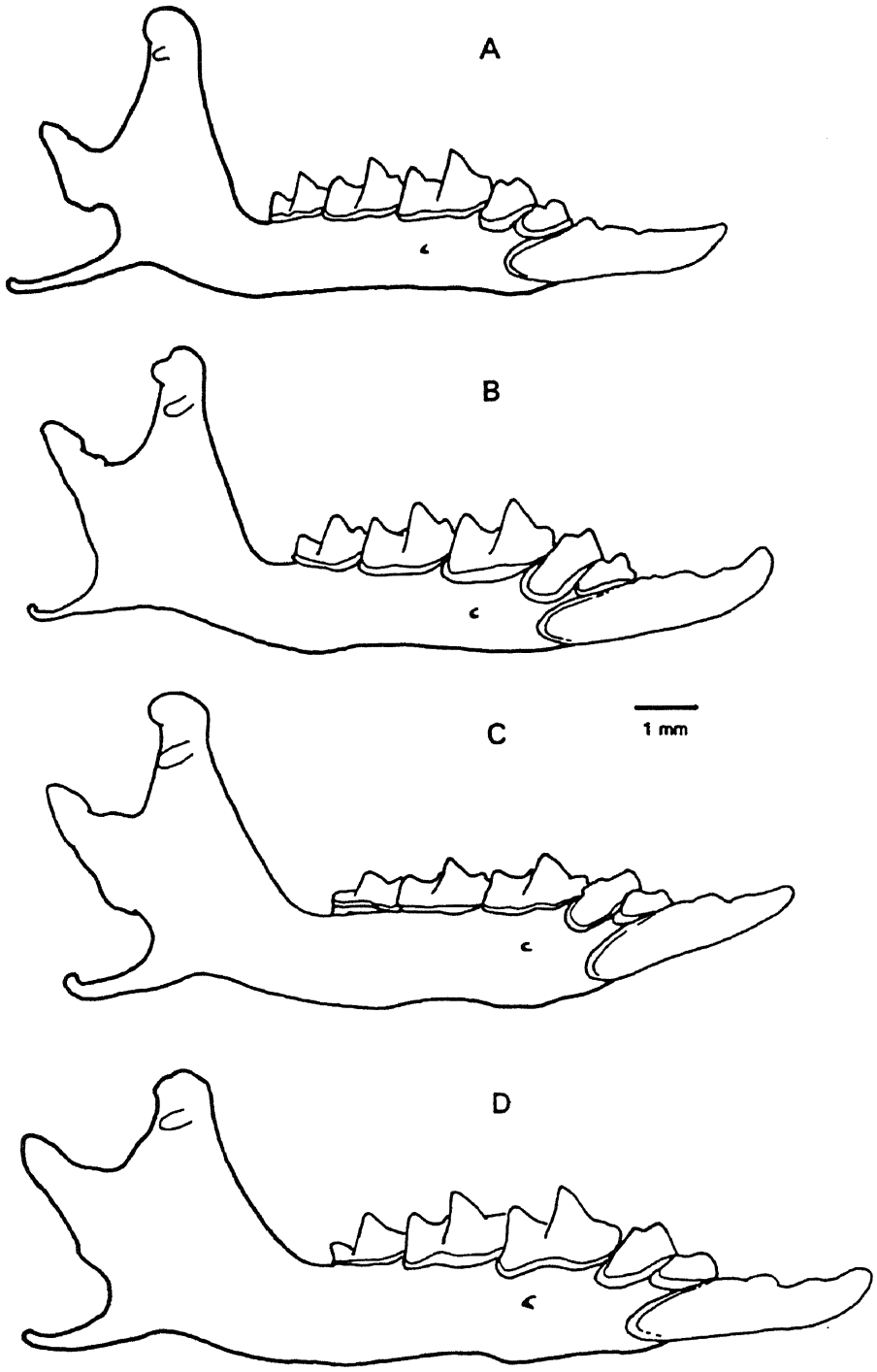

Figure 48. Labial view of right mandibles of Sorex tundrensis (A), Cryptotis nigrescens (B), C. mexicanus mexicanus (C), and C. thomasi meridensis (D).

present in some species.

6. Juncture of coronoid process with horizontal ramus: having a very steep slope (0; Fig. 48B); having a lesser slope (1; Fig. 48C, D). Polarized.

Shape of coronoid process.

The height of the coronoid process of the mandible generally is not highly variable among species of Cryptotis. One exception is in the C. gracilis group and Choate's (1970) C. thomasi group, which possess very low coronoid processes in contrast to other species. Width of the coronoid process in slightly more variable within species than height, but those of C. magna, C. mayensis, and C. merriami are very wide for the genus.

7. Height of coronoid process: normal (0; Fig. 48A, B, C); very low (1; Fig. 48D). Polarized.

8. Width of coronoid process near dorsal tip: narrow (0; Fig. 48B, C); wide (1; Fig. 48A). Unpolarized.

Shape of articular condyle.

Morphology of the articular condyle previously has been used to define subfamilies of the Soricidae and tribes of Soricinae (Repenning, 1967; Reumer, 1984), but I have found it to be variable within the genus Cryptotis. There is considerable variation among

species, but there is also considerable individual variation which makes it difficult to define the character exactly for each species. It is most useful to generalize the transformation series to two characters. In the plesiomorphic state, the ascending branch of the condyle is relatively low and wide, and the ventral articular facet is broad (Fig. 49A). In the apomorphic state, the ascending branch is tall and narrow, with a relatively shorter ventral articular facet (Fig. 49B).

9. Articular condyle: low and broad (0; Fig. 49A); high and narrow (1; Fig. 49B). Polarized.

Lower sigmoid notch.

The sigmoid notch, located between the base of the articular condyle and the angular process, can be either shallow (Fig. 50A) or deep (Fig. 50B) in Cryptotis. This transformation series also is variable among the outgroups, although most outgroup species inspected have a shallow notch. Neomys has a deep notch as in some Cryptotis. Sorex is unique in possessing an extremely deep notch, which extends beneath the entire ventral surface of the ventral facet of the articular condyle (Fig. 50C). However, this was treated as a deep notch (1) in establishing polarity for the hypothetical

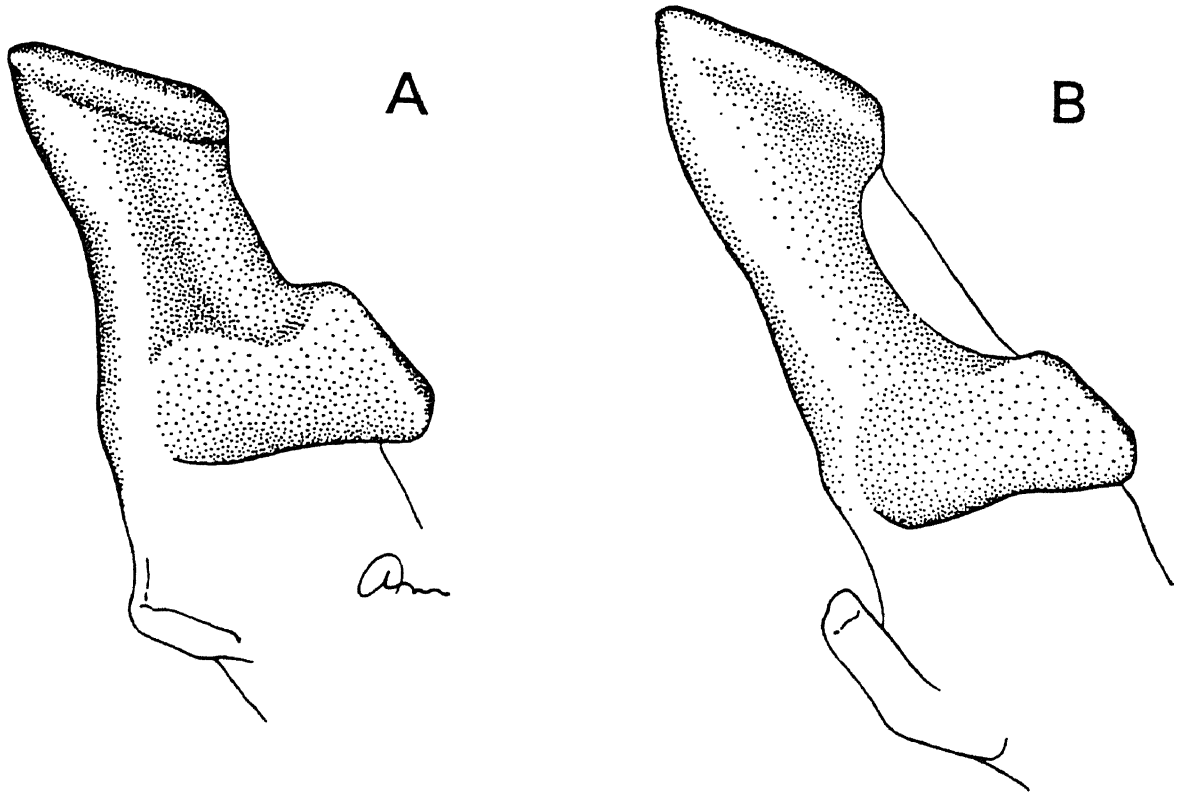

Figure 49. Oblique posterior view of articular condyles of C. merriami (A) and C. gracilis (B).

ancestor.

10. Lower sigmoid notch: shallow (0; Fig. 50A); deep (1; Fig. 50B); very deep (2; Fig. 50C; found only in Sorex). Polarized.

Number of visible unicuspids.

Nomenclature of dentition and dental characteristics follows Choate (1970).

In lateral view of the skull of some species of Cryptotis U4 is blocked from view by the paracone of P4, whereas in other species U4 is clearly visible. The closest outgroups, Blarina and Sorex, both possess more unicuspids than Cryptotis, making this transition series difficult to polarize exactly. In Sorex, all five unicuspids are visible in lateral view, but in Blarina only four are visible. It might be assumed that crowding of teeth, which results in P4 obscuring U4, forecasts loss of teeth and is thus apomorphic. However, I left this transformation series unpolarized.

11. Number of unicuspids visible in lateral view: all (0); last unicuspid hidden by P4 (1). Unpolarized.

Shape of unicuspids.

Among some species of Cryptotis there is a diminution in size of the cusps of U1 and U2. In the plesiomorphic

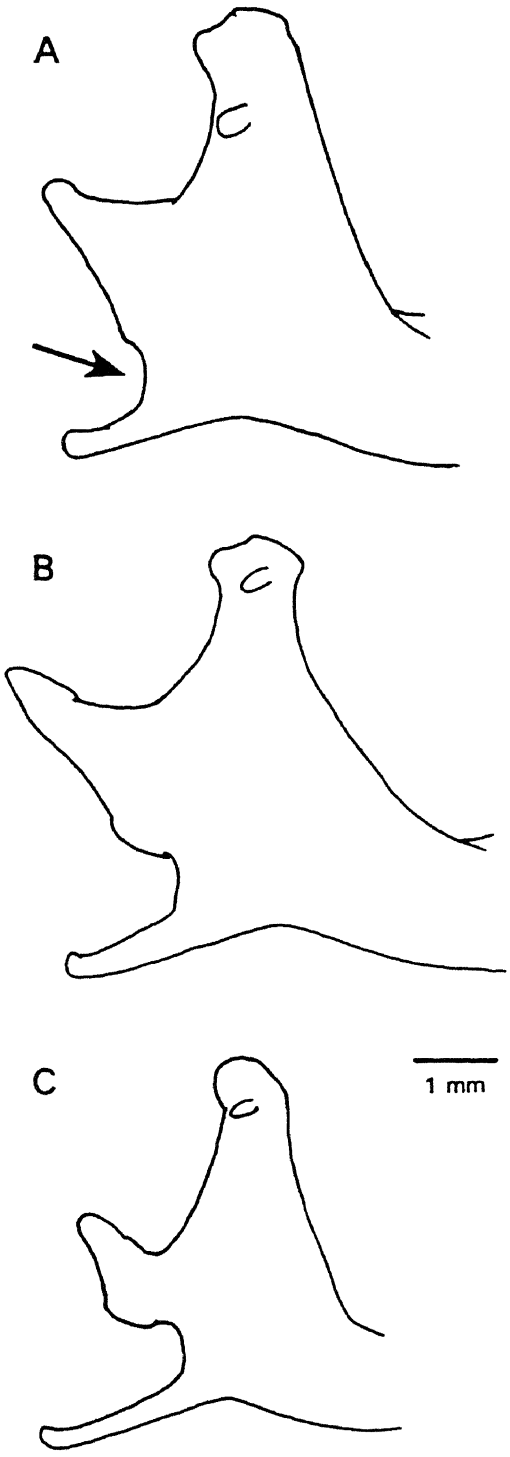

Figure 50. Labial view of posterior portion of right mandibles of C. merriami (A), C. goodwini (B) and Sorex tundrensis (C).

state a wide cusp derives from the entire base of the tooth, and both the anterior and posterior edges of the cusp clearly are convex. In its derived state (2) the cusp is very narrow and originates only from the anterior portion of the base. The posteroventral margin of the tooth clearly is concave. There also is what appears to be a clear intermediate state in which the cusp is reduced and the posteroventral margin is slightly concave (1). I hypothesized that these characters represent an ordered transition series. This is generally supported by ACCTRAN and DELTRAN character optimizations.

12. Shape of U1 and U2: cusp derives from all or almost all of base of tooth, posteroventral margin convex (0; Fig. 51A); low cusp derives from only a portion of base, posteroventral margin concave (1; Fig. 51B); high cusp derives from only a smaller portion of base, posteroventral margin very concave (2; Fig. 51C). Polarized.

Bulbous dentition.

I follow Choate (1970) in his usage of the term bulbous for the more massive dentition of some species of shrews. He noted that bulbous teeth appear more robust and have sides that are more convex-sided than

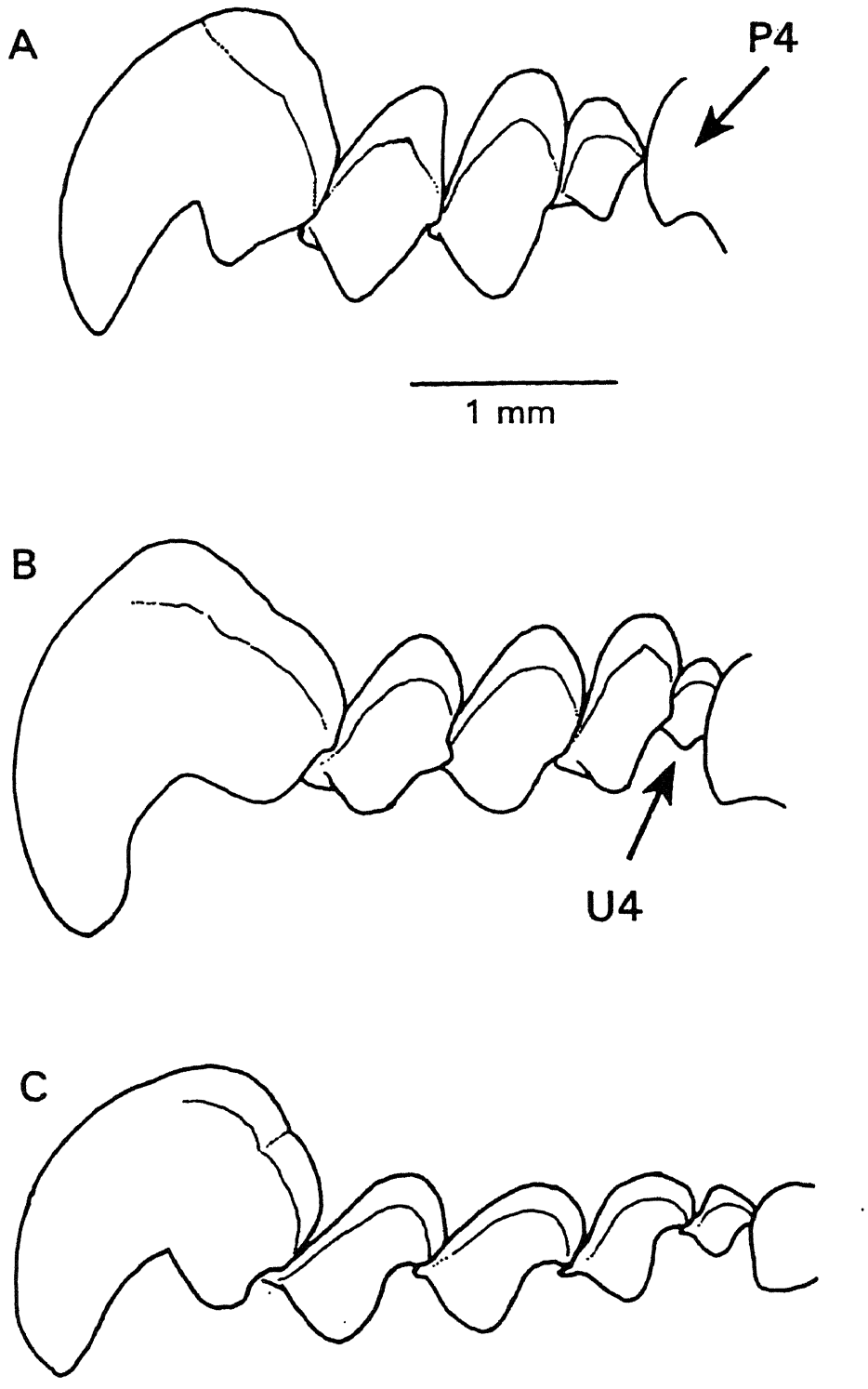

Figure 51. Labial view of left I1, U1-U4 of C. parva orophila, C. goldmani, and C. gracilis.

non-bulbous teeth. I agree with Choate that this transformation series is homoplastic, and it is difficult to polarize within the Soricinae. However, ACCTRAN and DELTRAN character optimizations using the outgroups to Cryptotis indicate that bulbous dentition is plesiomorphic for this genus.

13. Dentition: bulbous (0); not bulbous (1). Polarized.

Posterior emargination of P4, M1.

Choate (1970) noted the great variation in degree of concavity or recession of the posterior border of P4, M1, and M2. This is an extremely variable transformation series, both among species and among teeth. I chose use only P4 and M1, the emargination of which tends to match most closely. Emargination of M2 appears more independent. Choate (1970) suggested that plesiomorphically the upper dentition was not emarginate. Fossil and modern shrews outside the Soricinae and other animals with a W-shaped ectoloph, such as talpids and chiropterans, all tend to have highly emarginate dentition, suggesting that the filling in of this tooth and subsequent loss of the posterior concavity is apomorphic for shrews in general. However, multiple outgroup comparison indicates that emarginate dentition is apomorphic for Crypotis.

14. Posterior emargination of P4, M1: concave, but not particularly deep to only slightly concave (0); deep, nearly half way to hypocone (1). Polarized.

Relative size of anterior and posterior elements of M1.

In the ectoloph of M1 the valley separating the parastyle and mesostyle (anterior element) may be the same size as or smaller than the valley separating the mesostyle and metastyle (posterior element). Similarly, the protoconal and hypoconal basins of M1 may be approximately equal in size, or the protoconal basin may be reduced relative to the hypoconal basin. However, the relative size of the anterior and posterior portions of the ectoloph and the relative size of the protoconal and hypoconal basins do not vary together, nor do they exhibit the same patterns of distribution among species. For this reason, they are treated as separate transformation series.

Choate (1970) stated that C. mexicana and C. endersi possessed an unreduced anterior element of the ectoloph. My study of this character in these species indicates that both possess a reduced anterior element.

15. Ectoloph of M1 (Choate, 1970): anterior element reduced relative to posterior element (0); anterior and posterior elements equal in size (1). Polarized.

16. Protoconal basin of M1 (Choate, 1970): about equal in size to hypoconal basin (0); reduced relative to hypoconal basin (1). Polarized.

Morphology of M3.

The M3 is highly variable in morphology among species of Cryptotis, and among genera of soricids. Comparisons with reports on fossil taxa and with talpids and chiropterans suggests that M3 never was as fully developed in the Soricidae as either M1 or M2. Because of the difficulty in characterizing all of the variation present among and within species of Cryptotis, this transformation series was simplified to two characters, dependent upon the presence or absence of the metacone.

17. metacone on M3: present (0); absent (1). Unpolarized.

Shape of p3.

Plesiomorphically, p3 in buccal view is short anteroposteriorly, and it has a high anterior cusp (Fig. 52A). Some Cryptotis have an elongated p3 with a low, but distinct anterior cusp (Fig. 52B). Others, notably C. mayensis and C. merriami, have a reduced p3 with a very small anterior cusp. I hypothesized a priori that character (1) and character (2) probably had independent

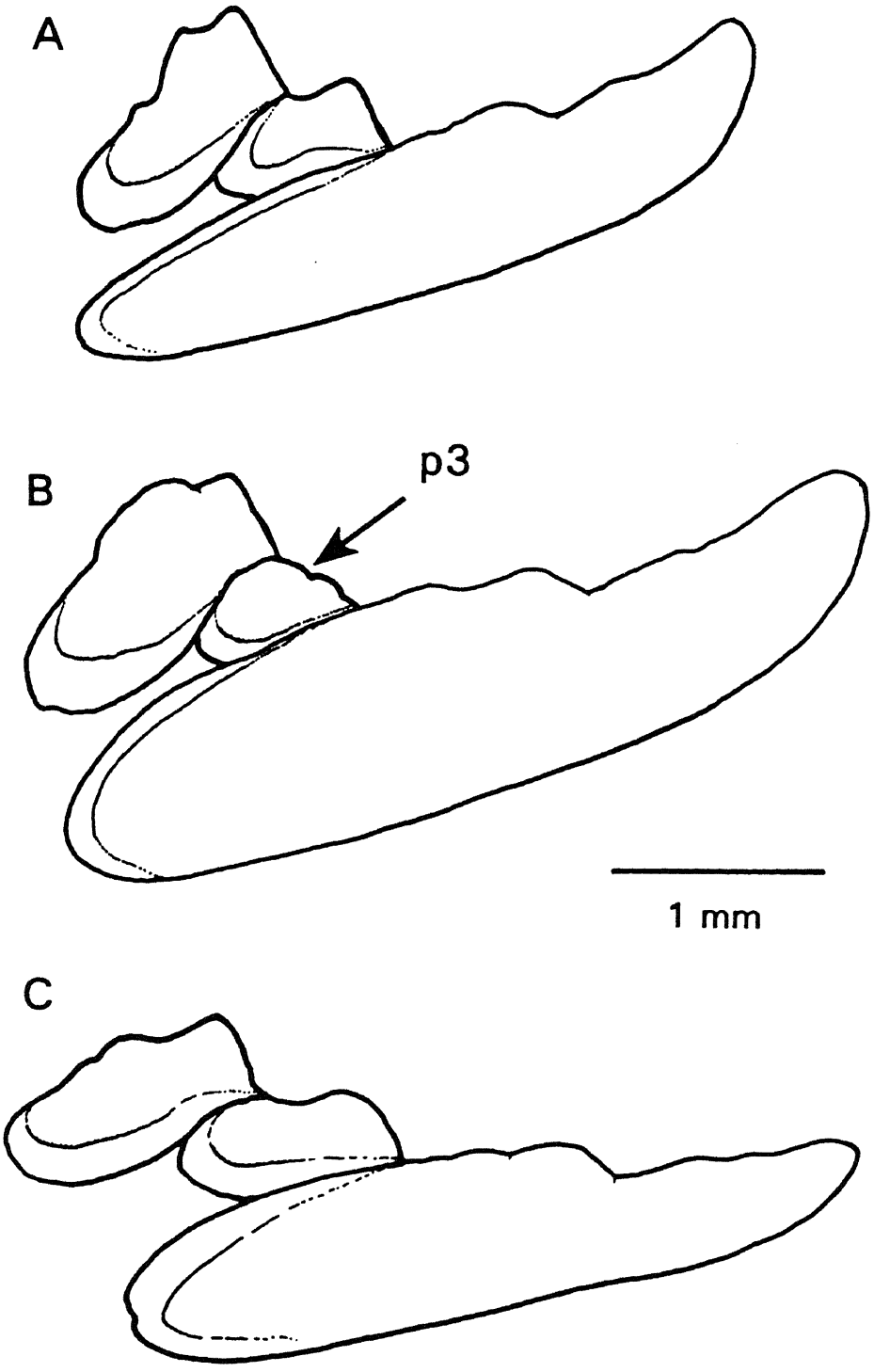

Figure 52. Labial view of right i1, p3, and p4 of C. parva parva (A), C. merriami (B), and C. gracilis (C). All three specimens are between age classes 1 and 2 of Rudd (1955).

derivations from character (0), and this was supported by the character optimizations.

18. shape of p3: short and high (0; Fig. 52A); reduced (1; Fig. 52B); long and low (2; Fig. 52C). Polarized.

Entoconid of m3.

Repenning used the lack of an entoconid in the talonid of m3 as a defining characteristic of the genus Cryptotis. However, as Choate (1970) pointed out, this is quite variable among species of Cryptotis. This also can vary within some species, such as members of the C. goldmani/goodwini complex (Woodman and Timm, manuscript a) and C. nigrescens (Woodman and Timm, manuscript b). There are three clear characters in what appears to be a well-ordered transition series ranging from a well-developed entoconid (0) to the talonid lacking an entoconid (2), with presence of a vestigial entoconid (1) appearing to be intermediate. However, this transition series shows a fair amount of homoplasy, and an orderly transition is not supported by ACCTRAN or DELTRAN character optimizations on the minimum-length trees.

19. Entoconid of m3 (Choate, 1970): present and well-developed (0); vestigial (1); absent (2). Polarized.

Results

The branch-and-bound tree-building algorithm resulted in 87 minimum-length trees of 48 steps each (see Appendix II). These trees each have a consistency index of 0.583, rescaled consistency index of 0.473, homoplasy index of 0.521, and retention index of 0.811.

The heuristic analysis carried out 1000 replications from random starting points. Each replication produced the same set of 87 trees as found by the branch-and-bound analysis, indicating that there is only a single island of most-parsimonious trees present for this data matrix. This conclusion is further supported by the high retention index. Data matrices with more than one island of minimum-length trees have low retention indices (Archie, 1989; Farris, 1989), and Maddison (1991) demonstrated experimentally that data matrices with only a single island have retention indices greater than 0.67.

Two transformation series were ignored by PAUP as uninformative: TS 4 and TS 14. Both transition series are autoapomorphic for C. parva, but are important because they are synapomorphic for the taxa considered as subspecies of C. parva.

Consensus Tree Topologies

Strict consensus and Adams consensus trees are presented in Figures 53 and 54. Consensus trees with the excluded taxa reinserted are shown in Figures 55 and 56. Both consensus trees indicate that there exist three main lineages within the genus Cryptotis: C. parva and its subspecies; C. nigrescens and related species (Cryptotis "D", C. hondurensis, C. magna, C. mayensis, C. mera, C. merriami); and C. thomasi and related species (Cryptotis "A", Cryptotis "B", Cryptotis "C", C. alticola, C. avia, C. endersi, C. equatoris, C. gracilis, C. jacksoni, C. goldmani, C. goodwini, C. griseoventris, C. mexicana, C. peregrina, C. squamipes). Relationships among these three groups are equivocal. The C. nigrescens group may be more closely related to the C. parva group or to the C. thomasi group. Both of these relationships are supported by minimum-length trees (Appendix II). However, the C. parva group and the C. thomasi group never are associated as sister taxa in any of the trees.

Both the strict and Adams consensus trees show similar topologies within the C. nigrescens group. Within this group, there is a polytomy among Cryptotis "D", C. hondurensis, C. mera, C. nigrescens, and a clade consisting of C. magna, C. mayensis, and C. merriami. Within this clade C. magna is the sister group to the

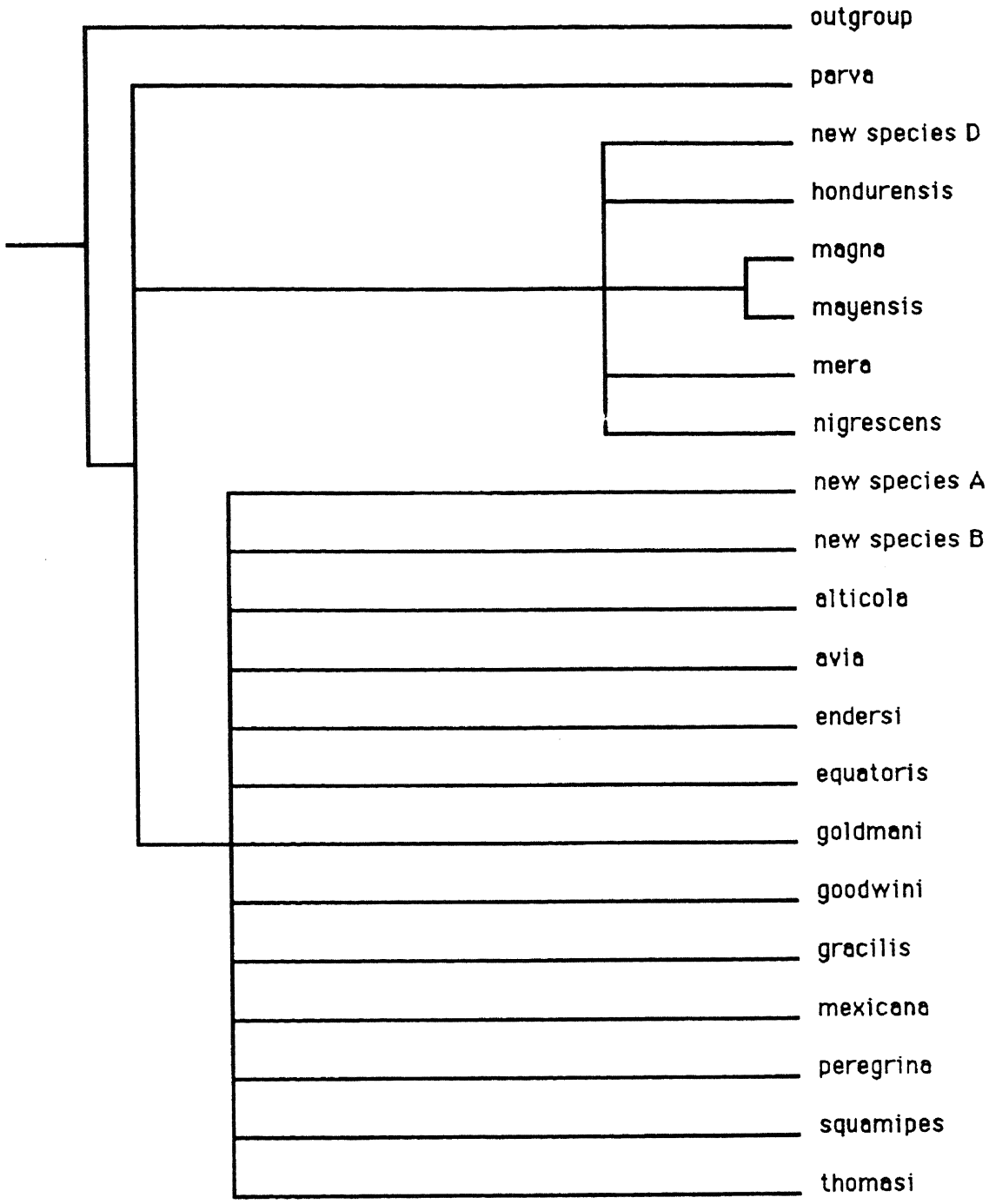

Figure 53. Strict consensus tree for Cryptotis.

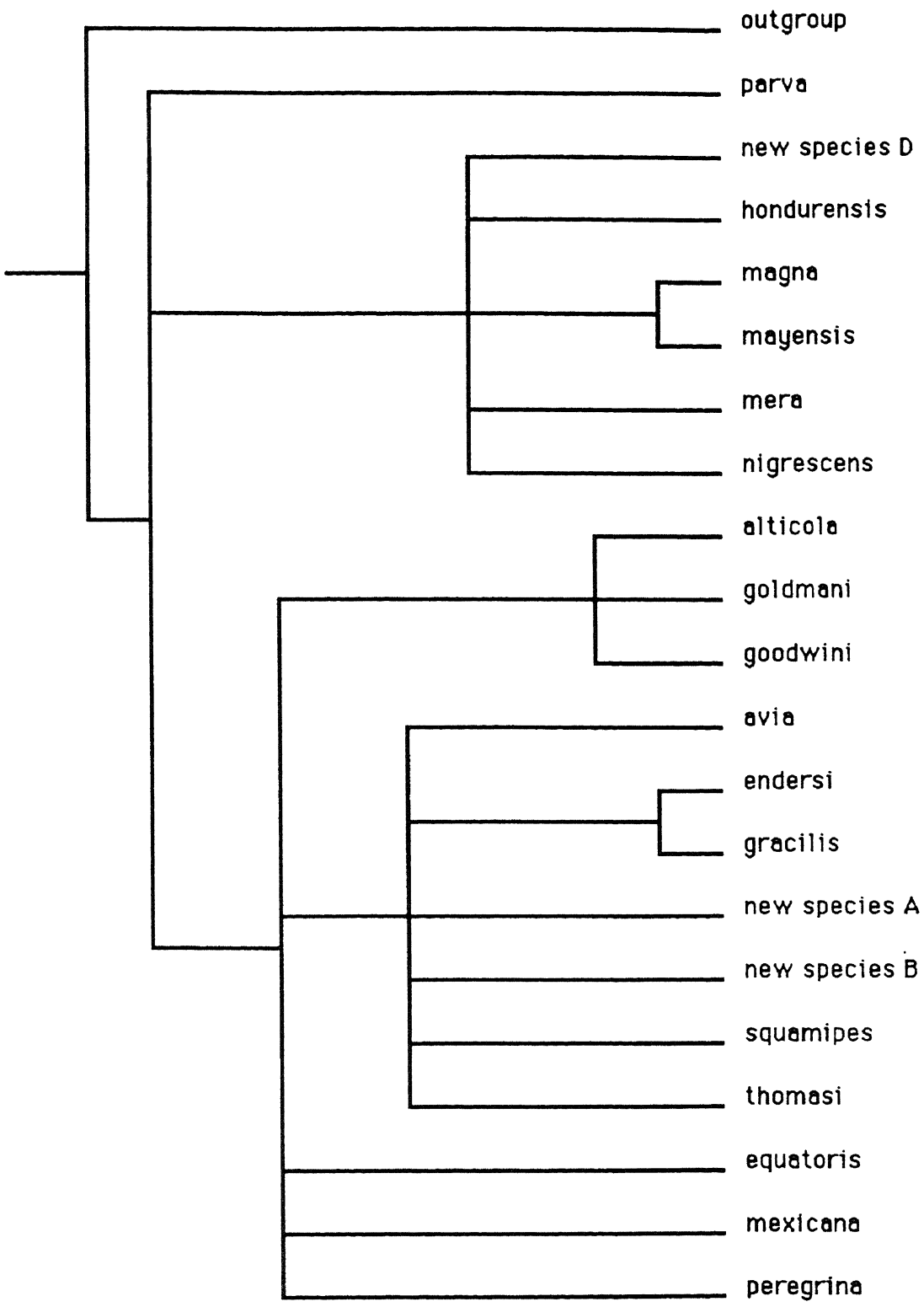

Figure 54. Adams consensus tree for Cryptotis.

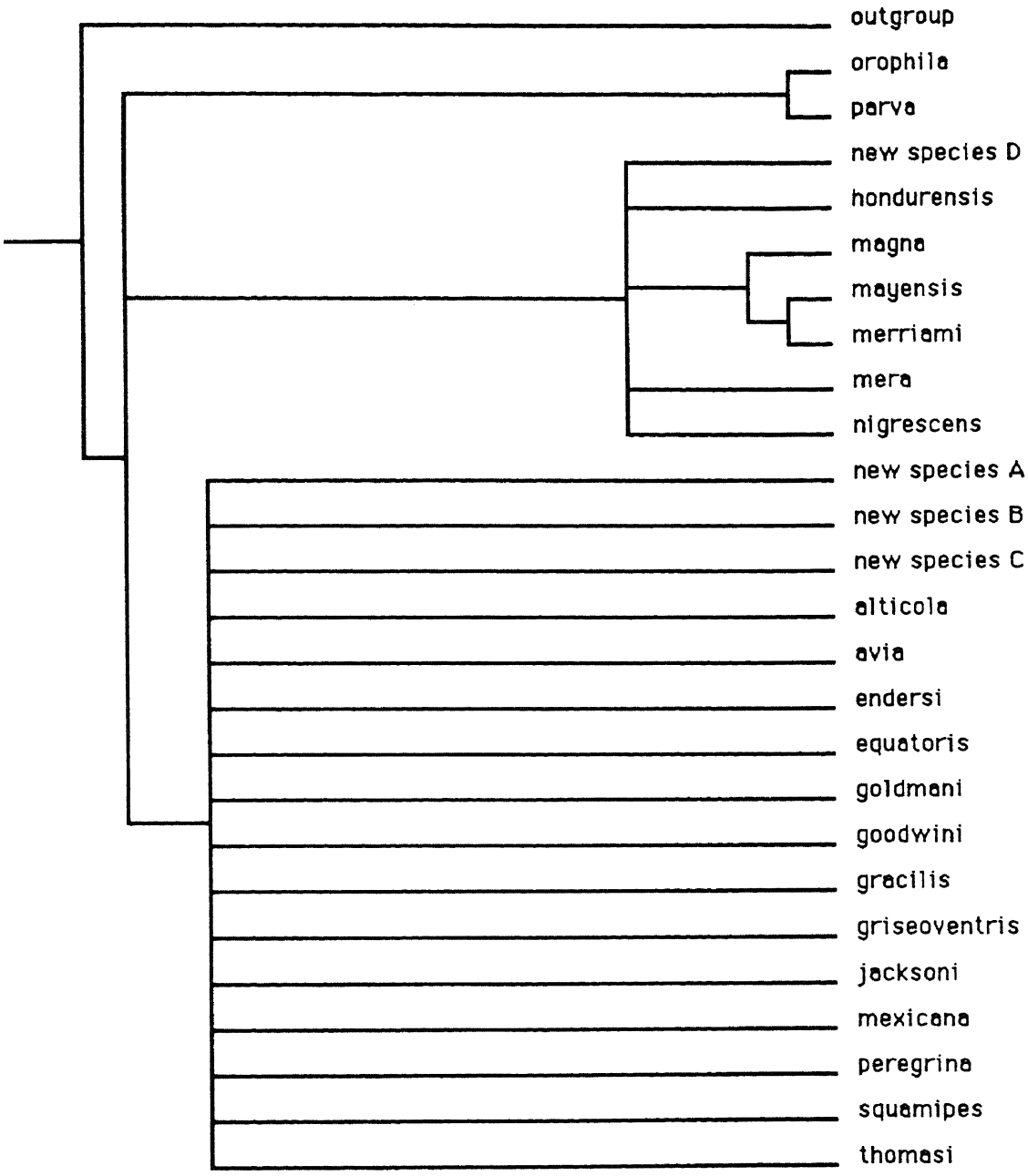

Figure 55. Strict consensus tree for Cryptotis with excluded taxa reinserted.

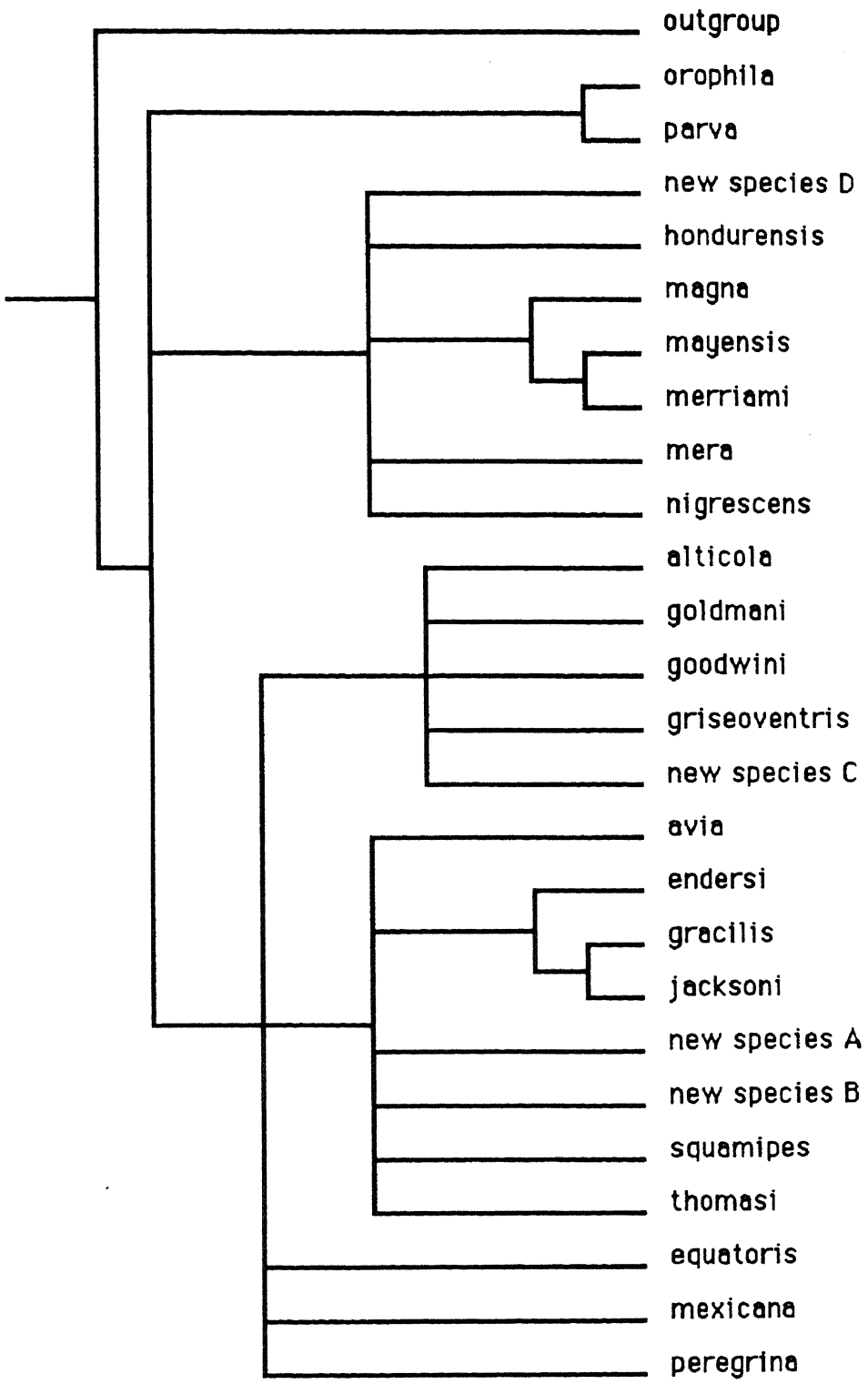

Figure 56. Adams consensus tree for Cryptotis with excluded taxa reinserted.

other two species. None of the minimum-length trees (Appendix II) support a topology as simple as that shown by the consensus trees. In some cases C. hondurensis and C. nigrescens are supported as sister species, and sometimes C. mera and Cryptotis "D" are shown as sister species.

There is disagreement between the two consensus trees in the topology of the C. thomasi portion of the tree. The strict consensus tree shows a polytomy among all members of the C. thomasi group, whereas the Adams consensus trees indicates that there are several non-varying associations among species. The species C. alticola, C. goldmani, C. goodwini, C. griseoventris, and Cryptotis "C" form a clade according to Adams consensus analysis. Cryptotis avia, C. endersi, C. gracilis, C. jacksoni, Cryptotis "A", Cryptotis "B", C. squamipes, and C. thomasi form a second clade. Within this grouping, C. endersi, C. gracilis, and C. jacksoni have a trichotomous relationship. There is tremendous variation within the C. thomasi clade among the most-parsimonious trees, and it is this variation which accounts for the large number of trees. However, none of these trees is as simplistic as either of the consensus trees. Further work is necessary to better determine relationships among the taxa in each of the

species groups.

Classification of the Species of Cryptotis

The listing of species within a genus in a particular classification generally attempts to reflect some idea about the relationships among those species. Recent attempts to present the species in the genus Cryptotis in a structured format (e.g., Hall, 1981; Nowak, 1991) relied upon Choate (1970) and Cabrera (1958), both of whom utilized some type of phenetic analyses. Below I present a revised classification of Cryptotis which attempts to reflect phylogeny (Wiley, 1979, 1981; Wiley et al., 1991) as inferred from the phylogenetic analysis reported in this manuscript. Informal species groups are used to separate individual higher level clades. Within species groups, species are grouped by lower level clades. Within polytomies, species are listed alphabetically. Cryptotis is treated as feminine in gender following Woodman (in press), and some species-level names have been changed to reflect this.

Family Soricidae

Subfamily Soricinae

Tribe Blarinini

Genus Cryptotis

C. parva group

C. parva

C. nigrescens group

Cryptotis "D"

C. hondurensis

C. magna

C. mayensis

C. merriami

C. mera

C. nigrescens

C. thomasi group

C. alticola

C. goldmani

C. goodwini

C. griseoventris

Cryptotis "C"

C. avia

C. endersi

C. gracilis

C. jacksoni

Cryptotis "A"

Cryptotis "B"

C. montivaga

C. squamipes

C. thomasi

C. equatoris

C. peregrina

C. mexicana

Cryptotis montivaga is included in the South American clade of the C. thomasi group based on certain characters that it shares with that group. However, its characters are not known for all tranformation series used in my analysis, and the species may prove to belong elsewhere in the classification.

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Woodman, N., and R. M. Timm. manuscript b. Intraspecific and interspecific variation in the Cryptotis

nigrescens species complex of small-eared shrews (Insectivora: Soricidae), with the description of a new species from Colombia.

SUMMARY AND CONCLUSIONS

The systematics and biogeography of small-eared shrews of the genus Cryptotis rarely have been studied, and the genus is poorly known biologically. Merriam (1895) undertook the first comprehensive treatment of Cryptotis, as a subgenus of Blarina. At that time he recognized twelve species of Cryptotis, seven of which he described in that work. Before Choate's (1970) revision of the Middle American members of the genus Cryptotis, there were 29 recognized species (Cabrera, 1958; Hall and Kelson, 1959). Choate combined a large number of Mexican and Central American taxa, reducing the total number to twelve species. Since the time of Choate's work, the number of specimens of Cryptotis in systematic collections has increased greatly, making possible a more comprehensive review of the species in this genus.

My study of morphological variation and the elevational and geographic distributions of three groups of small-eared shrews (C. gracilis group, C. goldmani group, and C. nigrescens group) resulted in the following conclusions:

1. A single specimen of C. gracilis previously reported

from Honduras, far outside the main known range of this species group in Costa Rica and Panama, represents a distinct and unrelated species, recently described as C. hondurensis (Woodman and Timm, 1992). This species appears to be most closely related to C. nigrescens (sensu stricto).

2. Small-eared shrews previously identified as C. gracilis in Costa Rica and Panama now are recognized as a complex of four species restricted to high elevation environments: C. gracilis (sensu stricto) is distributed in the Talamancan Highlands of Costa Rica and adjoining Chiriquí Highlands of Panama; C. jacksoni occurs on Volcán Irazú and adjoining Volcán Turrialba in Costa Rica; Cryptotis "A" is found on Volcán Barva in Costa Rica; and Cryptotis "B" inhabits the Costa Rica's Tilarán Cordillera. These four species may not form a natural group, but all are members of the C. thomasi species group.

3. Members of the C. goldmani complex are distinguished by their enlarged forefeet and claws. Originally placed in two species, I now recognize five species, all of which occur only at high elevations: C. alticola ranges in the highlands of central Mexico; C. goldmani (sensu stricto) occurs only in the Mexican States of Guerrero

and Oaxaca; C. griseoventris is known from the northern sierra of the Mexican State of Chiapas and adjoining highlands in Guatemala; C. goodwini, is found in the southern Sierra Madre of Chiapas and through much of Guatemala and the northern corner of El Salvador; Crypotis "C" inhabits highlands in central Honduras. These five species appear to form a monophyletic group, although relationships among them are not worked out yet.

4. The C. nigrescens group is a complex and speciose collection of small-eared shrews. Previously considered a single, wide-ranging species, I now recognize five species previously referred to C. nigrescens: C. mayensis is mostly restricted to the lowlands of the Yucatan Peninsula, with the exception of a record from a single owl pellet sample in Guerrero. The Guerrero specimens eventually may prove to belong to a distinct species once complete specimens are known, but for now are referred to C. mayensis. Cryptotis mayensis is the only species of Cryptotis restricted entirely to lowland habitats. Cryptotis merriami is known from highlands in Chiapas, Guatemala, El Salvador, Honduras, and northern Nicaragua, with a disjunct population in northern Costa Rica. Many isolated populations occur within this group, and it may prove to be even more complex than now

considered. Cryptotis nigrescens (sensu stricto) is restricted to populations occurring in adjoining highlands in Costa Rica and western Panama. Cryptotis mera is known from two islolated mountaintops along the Panama/Colombia border. Cryptotis "D" inhabits highlands in the Central Cordillera of Colombia. Its presence in the Cordillera Central suggests the likelihood of a species of the C. nigrescens group occurring in Colombia's Cordillera Occidental. The five species previously placed in the C. nigrescens species complex do not form a natural group by themselves. My analysis suggests that C. hondurensis and C. magna also belong in this group. Cryptotis magna is most closely related to a clade consisting of C. mayensis and C. merriami. In addition, Cryptotis hondurensis and C. nigrescens (sensus stricto) may be sister species. Other relationships within this monophyletic group of seven species remain to be worked out.

5. Relationships among species of the genus Cryptotis are complex and are incompletely resolved. My analysis, based on construction of the most-parsimonious tree from a data matrix of 19 transition series containing 44 characters, indicates three distinct, supported lineages: 1) the C. parva group, consisting of C. parva

and its subspecies; 2) the expanded C. nigrescens group of seven species; and 3) a clade consisting of the expanded C. thomasi group, which includes all members of Choate's (1970) C. mexicana and C. thomasi groups and the seemingly paraphyletic C. gracilis group. Cryptotis peregrina and C. equatoris, previously considered subspecies of C. mexicana (Choate, 1970; Hall, 1981) and C. thomasi, respectively (Cabrera, 1958), are recognized as distinct species on the basis of characters defined in my analysis. A comprehensive review of the members of this clade is warranted.

I classify the 25 recognized species of Cryptotis into three informal, but informative species groups: 1) the restricted C. parva group, which includes the seven to nine taxa now considered subspecies of C. parva; 2) the expanded C. nigrescens group, which includes Cryptotis "D", C. hondurensis, C. magna, C. mayensis, C. mera, C. merriami, and C. nigrescens,; and the expanded C. thomasi group, including Cryptotis "A", C. alticola, C. avia, Cryptotis "B", Cryptotis "C", C. endersi, C. equatoris, C. goldmani, C. goodwini, C. gracilis, C. griseoventris, C. jacksoni, C. mexicana, C. montivaga, C. peregrina, C. squamipes, and C. thomasi. Each of these groups differs in composition from Choate's (1970) concept of these groups. His "relict species" group was

paraphyletic, and the species clearly are members of other groups.

There is one species of Cryptotis known to occur in the United States, nine in Mexico, two in Belize, five in Guatemala, three in El Salvador, four in Honduras, two in Nicaragua, seven in Costa Rica, four in Panama, one in Venezuela, four in Colombia, two in Ecuador, and one in Peru.

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APPENDIX I

HISTORICAL REVIEW OF *CRYPTOTIS*

The shrews, Family Soricidae, have a complex taxonomic history, spanning more than two centuries of rearrangement by natural historians and biologists (Gill, 1875). Linné (1758) named the first genus, *Sorex*, of what we now call the Soricidae, placing it in the order Bestiae along with *Sus*, *Dasypus*, *Erinaceus*, *Talpa*, and *Didelphis*. He referred three species to the genus *Sorex*: the type species, *S. araneus*, *S. aquaticus* [= *Scalopus aquaticus*], and *S. cristatus* [= *Condylura cristata*]. For at least 65 years following Linné (1758), *Sorex* was the only widely recognized genus of shrews. The first New World members of the modern family were added when Kerr (1792) named the taxa *S. arcticus* and *S. arcticus cinereus* [= *S. cinereus*].

North American short-tailed shrews of the genera *Cryptotis* and *Blarina* normally have been closely associated in taxonomic arrangements since Say (1823) described the first two species, *S. brevicaudus* [= *Blarina brevicauda*] and *S. parvus* [= *Cryptotis parva*]. When Gray (1838) split *Sorex* into five genera (*Corsira*, *Myosorex*, *Sorex*, *Amphisorex*, and *Crossopus*), he separated the known North American soricids among two of the new genera: *Corsira*, which consisted of some

northern European and most North American Sorex [including Blarina and Cryptotis], and Amphisorex, in which he included Sorex palustris along with some European shrews. Sorex was restricted to include only a few European species. Gray (1838) subdivided his new genus Corsira to include a new subgenus, Blarina, consisting only of the North American short-tailed shrews [Cryptotis and Blarina].

According to Merriam (1895:5), Lesson (1842) elevated Blarina to full generic rank. However, in Lesson's classification Blarina and Amphisorex are subdivisions of the subgenus Corsira within the genus Sorex. Lesson's (1842:88-89) inconsistent use of the names creates confusion, however. For example, Blarina brevicaudata (sic), which by his classification correctly should be called Sorex (Corsira) brevicaudus, is found under the subdivision Blarina. Yet Corsira Forsteri (sic), which under this classification should be Sorex (Corsira) forsteri, is found in subdivision Amphisorex.

It appears that Gray (1843a) was the first to recognize Blarina as a separate genus, although he spelled it "Blaria", listing "Blarina, Lesson" as a synonym. Baird (1857, 1858) also recognized Blarina as a distinct genus, and he was the first to both use it as

such and spell it correctly. Based on the number of teeth and uniformity of pelage coloration, Baird subdivided Blarina into two informal groups corresponding to the 30-toothed forms [= Cryptotis] and 32-toothed forms [= Blarina]. He suggested that these might be considered subgenera, but did not name them. These two divisions were accorded formal subgeneric status by Coues (1877), who separated them under the names Blarina and Soriciscus. In his comprehensive revision of the short-tailed shrews, Merriam (1895) also recognized the subgeneric division of Blarina, but noted that the name Soriciscus Coues (1877), was antedated by Cryptotis Pomel (1848), and he renamed it appropriately. Pomel (1848) originally named Cryptotis as a "section" (equivalent to a subgenus) of the genus Musaraneus Brisson (1762). In his arrangement Pomel also had separated Cryptotis and Blarina, but as sections (= subgenera) of different genera.

Blarina continued to be used as the genus for all North American short-tailed shrews at least until 1908 (e.g., Trouessart, 1898-1899, 1904-1905; Elliot, 1901; Stone, 1908). Cryptotis was raised to generic rank without formal treatment. Apparently, the first published usage of Cryptotis as a genus is G. S. Miller's (1911) paper, "Three new shrews of the genus

Cryptotis". The following year Goldman (1912) and Miller (1912) used Cryptotis as a genus, as did Thomas (1921), G. M. Allen (1923), Cabrera (1925), and Jackson (1933). Some workers continued to treat Cryptotis as a subgenus of Blarina as late as 1921 (J. A. Allen, 1912; Cory, 1912; Thomas, 1912; Stone, 1914; Gaumer, 1917; Anthony, 1921). Cryptotis now is accepted universally as a distinct genus of short-tailed shrews, commonly called the small-eared or least shrews (Miller and Kellogg, 1955; Cabrera, 1958; Hall and Kelson, 1959; Choate 1970; Hall, 1981; Honacki et al., 1982; Corbet and Hill, 1991; Nowak, 1991).

Gender of Cryptotis

Despite nearly a century of continual usage, the question of the correct gender of the generic name Cryptotis had not been addressed formally, and in the past taxonomists variously treated Cryptotis either as masculine or feminine in naming new species and subspecies. Although many of the species names associated with Cryptotis are feminine, most of these were described when Cryptotis was considered a subspecies of Blarina, which is feminine. Goldman (1912: C. merus), Thomas (1921: C. medellinius), and Goodwin (1954a: C. tersus; 1956: C. celatus) all

associated masculine species names with the genus. Miller (1911) similarly gave the subspecies C. pergracilis macer a masculine name, although Miller and Kellogg (1955:39) later listed this name as macra, possibly in an attempt to feminize the name. Cabrera (1958), in his compendium of South American mammals, clearly considered the genus masculine, and he combined Cryptotis with the masculinized trivial names avius and montivagus. Although he made these changes without comment, Cabrera's inclusion of the feminine spellings in his synonomies for the respective species indicates that he made the changes consciously. In contrast, Choate (1970), Corbet and Hill (1980, 1991), Hall (1981), and Honacki et al. (1982) all treated Cryptotis as feminine in gender. Currently, the most widely cited species in the genus is the common North American small-eared shrew, Cryptotis parva. The specific epithet, parva, is clearly feminine.

Other mammalian generic names with -otis endings face similar problems. The peramelid marsupial genus, Macrotis traditionally has been treated as feminine. In contrast, the South American rodent genus Phyllotis and the cosmopolitan bat genus Myotis, currently are combined with either masculine (e.g., P. amicus, P. caprinus, M. adversus, M. lucifugus) or neuter (P.

andium, M. altarium) names (Honacki et al., 1982).

Greek noun formation dictates that names ending in -otis are feminine (Woodman, in press). This ending comes from the Greek word, otis, a derived combining form of the neuter noun otos ("ear"). Cryptotis, for example, is a combination of the two Greek words kryptos ("hidden") + otis. The gender of such a combining form is determined by the stem formative, which in this case is otid-. Forms in -otis (nominative) and -otidos (genetive) are feminine derived nouns (H. D. Cameron, in. litt.). For example, aefotis, which literally means, "having two ears", is a feminine noun referring to a two handled pail or a covering for the ears. The Greek feminine noun otis (genetive: otidos) means "feminine eared creature" and refers to the bustard. Perhaps ornithologists recognized this early on. All genera with -otis endings in the avian family Otidae, the bustards (Afrotis, Choriotis, Chlamydotis, Eupodotis, Lissotis, Lophotis, Neotis, Otis), are treated as feminine.

Article 31b of the International Code of Zoological Nomenclature (Ride et al., 1985) requires that species names agree in gender with the generic names with which they are combined. Thus, the above mentioned specific names associated with Cryptotis must be spelled celata,

macera, medellinia, mera, parva, and tersa. The names combined with Phyllotis, are correctly spelled amica, andia, and caprina. Those with Myotis are correctly adversa, altaria, and lucifuga.

Type Specimens of Cryptotis

The following is a list of all formally proposed names for species and subspecies, both Recent and fossil, currently recognized as belonging to the mammalian genus Cryptotis. The purpose of this listing is to provide ready access to all proposed names for species of Cryptotis, the publications in which the names first formally appeared, and synonomy of the proposed names with currently recognized taxa. This is especially important because there has not been a comprehensive revision of the genus since Merriam (1895). Choate (1970) provided an extensive treatment of Mexican and Central American species, but South American and North American taxa have received only cursory treatments without explanation (Cabrera, 1958; Hall, 1981; Honacki et al., 1982).

In addition to proposed names of shrews now recognized as Cryptotis, I have included some species names which belong to taxa now recognized as synonyms of species in other genera. Examples of this include Blarina costaricensis and B. pyrrhonota, the type

localities of which were originally reported as Costa Rica (Allen, 1891) and Surinam (Gmelin, 1789), respectively. These forms were based on specimens from the United States and Europe mixed in with Latin American collections (Merriam, 1895; Husson, 1963). Because the type areas are far south of the well established ranges of Blarina, these taxa might easily be confused as species of Cryptotis (e.g., Cabrera, 1958).

The following list is organized alphabetically, first by genus, then species, and finally subspecies. Subgeneric designations are ignored in ordering the list. Information for each currently recognized species is included under the name for that taxon as it was originally proposed. Where available, this information includes author, date of publication, museum collection number of the holotype, type locality, and synonomy with presently recognized scientific name if it is different from the original designation. Type localities are given as they appeared in the original descriptions, with emendations in brackets. A cross reference is provided for currently recognized taxa which were originally named something else. For example, Cryptotis parva berlandieri is cross referenced to Blarina berlandieri, which is the name the holotype bears.

Currently recognized names for taxa are designated by a cross (+) before the name. Extinct species known only from fossils are designated on the list by a double asterisk (**) after the name. Holotypes of Cryptotis are under the care of the following institutions: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); The Natural History Museum [formerly the British Museum (Natural History)], London (BMNH); Cleveland Museum of Natural History, Cleveland (CMNH); Field Museum of Natural History, Chicago (FMNH), University of Kansas Museum of Natural History, Lawrence (KU); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); University of Michigan Museum of Paleontology, Ann Arbor (UMMP); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico, D.F. (IBUNAM); U.S. National Museum of Natural History, Washington (USNM).

Types of Cryptotis

+Blarina J. E. Gray, June 1838:124.

Type species: Sorex talpoides Gapper [= Blarina brevicauda talpoides].

Comments: Gray proposed Blarina, which then included

Sorex parvus [= Cryptotis parva], as a subgenus of his genus Corsira [= Sorex, in part]. Baird (1858) later elevated Blarina to generic level.

Blarina adamsi**, C. W. Hibbard, January 1953:29.

Holotype: UMMP 27267.

Type locality: University of Michigan locality UM-K1-47, in Fox Canyon, sec. 35, T.34 S, R.30 W, Meade County, Kansas.

Age: late Pliocene (early Blancan).

Stratigraphic interval: upper Pliocene Rexroad Fm., Rexroad fauna.

Comments: Retention of a minute P^2 gives this shrew the dental formula of living Blarina (32 teeth in contrast to 30 in living Cryptotis). However, based on mandibular structure and features of the upper and lower dentition, Repenning (1967:39-40) considered it most appropriate to consider B. adamsi a species of Cryptotis. This assignment was agreed with by Choate (1970) and Jones et al. (1984).

Blarina alticola, C. H. Merriam, 31 December 1895:27.

Holotype: USNM 52047.

Type locality: Mount Popocatepetl, Mexico (altitude, 11,500 feet). [Volcán Popocatepetl, State of Mexico]

Collected: 25 February 1893, by E. W. Nelson (field

no. 4396).

Comments: This is now Cryptotis alticola.

Blarina berlandieri, S. F. Baird, 14 July 1858:53.

Lectoype: USNM 2159, designated by Lyon and Osgood (1909:237).

Type locality: vicinity of Matamoras. [Tamaulipas, Mexico]

Collected: probably by J. L. Berlandier, presented to the U.S. National Museum by D. N. Couch.

Comments: This is presently considered to be Cryptotis parva berlandieri (Davis, 1941:413).

Blarina costaricensis, J. A. Allen, 17 April 1891:205.

Holotype: AMNH 3642/2800.

Type locality: La Carpintera. [Cerro La Carpintera; 8 mi E of San José; Cartago Province; Costa Rica (but see below)]

Collected: October 1890 by George K. Cherrie (but see below).

Comments: Surprised to find a species of Blarina so far south of its known range, Allen wrote to the holotype's collector, G. K. Cherrie, to see if the locality given was in error. "He replied emphatically in the negative, the specimen having been taken by himself in Costa Rica at the locality

above stated" (Allen, 1891:206; see also Allen, 1897:34). However, in 1895 Merriam identified the type specimen as a B. brevicauda and suggested that it probably came from Iowa, where the collector lived before going to Costa Rica (Merriam, 1895:12). Since then, the type locality usually is reported as the "upper Mississippi Valley". I concur that the holotype clearly is a Blarina.

Blarina equatoris, O. Thomas, April 1912:409.

Holotype: BMNH 99.9.9.3.

Type locality: Ecuador: Sinche, Guabanda, 4000 m. [Sinchig; 9 km N Guaranda; Bolívar Prov.; Ecuador]

Collected: 17 December 1898, by Perry O. Simons.

Comments: Chubb (1919), reporting on birds collected by Perry O. Simons from the same locality as the type of B. equatoris on the same dates, recorded the locality as, "Sinche, Guaranda" in Guayas Province. In contrast, Cabrera (1958) placed Sinche in Chimborazo Province. Paynter and Traylor (1977:118) provide the locality as reported in brackets above. This concurs with the NIS gazetteer for Ecuador.

The taxon currently is Cryptotis thomasi equatoris (Cabrera, 1958:47).

Blarina exilipes, S. F. Baird, 14 July 1858:51.

Lectotype: USNM 2157, designated by Lyon and Osgood (1909:237).

Type locality: Washington, Miss. [Washington; Adams Co.; Mississippi]

Collected: by B. L. C. Wailes.

Comments: This is a synonym of Cryptotis parva parva (Hall and Kelson, 1959:58).

B[larina]. eximius, S. F. Baird, 14 July 1858:52.

Comments: Baird proposed this taxon as an eventuality, stating, "It is quite possible that further investigations and fuller collections will separate the St. Louis and Illinois specimens from the rest [of B. exilipes], in which event they may bear the name of B. eximus" (Baird, 1858:52). No holotype was designated, but his comments were based on a study of two USNM specimens, skin number ?639 (sic), paired with skull number 1790, from St. Louis, Missouri, and skin number ?2166 (sic), paired with skull number 3109 from DeKalb Co., Illinois. As with B. exilipes, this is a synonym of Cryptotis parva parva (Hall and Kelson, 1959:58).

Blarina floridana, C. H. Merriam, 31 December 1895:19.

Holotype: USNM 16510/23937.

Type locality: Chester Shoal, 11 miles north of Cape

Canaveral, Brevard County, Fla. [Florida]

Collected: 22 April 1889, by Morris M. Green (original no. 44).

Comments: This is now Cryptotis parva floridana (Harper, 1927:270).

Blarina fossor, C. H. Merriam, 31 December 1895:28.

Holotype: USNM 68545.

Type locality: Mount Zempoaltepec, Oaxaca, Mexico (altitude, 10,500 feet). [Cerro Zempoaltepec]

Collected: 10 July 1894, by E. W. Nelson and E. A. Goldman (original no. 6419).

Comments: This is a synonym of Cryptotis goldmani.

Blarina magna, C. H. Merriam, 31 December 1895:28.

Holotype: USNM 68575.

Type locality: Totontepec, Oaxaca (altitude, 6,800 feet).

Collected: 24 July 1894, by E. W. Nelson and E. A. Goldman (original no. 6493).

Comments: This is now Cryptotis magna (Miller, 1912:28). The USNM catalog gives the locality as Mt. Zempoaltepec, but the skin tag on the holotype gives it as Tontotepec, a Mije Indian village on Cerro Zempoaltepec (Goldman, 1951).

Blarina mayensis, C. H. Merriam, 29 November 1901:559.

Holotype: USNM 108087.

Type locality: a Maya ruin at Chichenitza, Yucatan. [Chichén Itzá]

Collected: 5 February 1901, by E. W. Nelson and E. A. Goldman (original no. 14495).

Comments: This is now Cryptotis mayensis.

Blarina meridensis, O. Thomas, 1898:457.

Holotype: BMNH 98.5.15.5.

Type locality: Merida, alt. 2165 m. [State of Merida, Venezuela]

Collected: by S. Briceno.

Comments: This is now Cryptotis thomasi meridensis (Cabrera, 1958:48).

Blarina (Soriciscus) mexicana, E. Coues, 15 May 1877:652.

Holotype: USNM 3525/4438.

Type locality: Xalapa, Mexico. [Jalapa, State of Veracruz]

Collected: purchased from R. Montis d' Oca.

Comments: This is now Cryptotis mexicana mexicana (Miller, 1911:221).

Blarina mexicana goldmani, C. H. Merriam, 31 December 1895:25.

Holotype: USNM 70244.

Type locality: mountains near Chilpancingo, Guerrero, Mexico (altitude, 10,000 feet) [Poole and Schantz, 1942, give the elevation as 9,600 ft.]

Collected: 23 December 1894, by E. W. Nelson and E. A. Goldman (original no. 7231).

Comments: This is now Cryptotis goldmani.

Blarina mexicana machetes, C. H. Merriam, 31 December 1895:26.

Holotype: USNM 71456.

Type locality: mountains near Ozolotepec, Oaxaca (altitude, 10,000 feet).

Collected: 26 March 1895, by E. W. Nelson and E. A. Goldman (original 7723).

Comments: This is a junior synonym of Cryptotis goldmani.

Blarina mexicana peregrina, C. H. Merriam, 31 December 1895:24.

Holotype: USNM 68317.

Type locality: mountains 15 mi W of city of Oaxaca, Mexico (altitude, 9500 feet).

Collected: 12 September 1894, by E. W. Nelson and E. A. Goldman (original no. 6748).

Comments: This is now Cryptotis mexicana peregrina

(Miller, 1911:222).

Blarina montivaga, H. E. Anthony, 3 November 1921:5.

Holotype: AMNH 47200.

Type locality: Bestion, Prov. del Azuay, Ecuador; altitude 10,000 ft.

Collected: 15 January 1921, by H. E. Anthony.

Comments: This is now Cryptotis montivaga (Cabrera, 1925:134).

Blarina nelsoni, C. H. Merriam, 31 December 1895:26.

Holotype: USNM 65437.

Type locality: Volcano of Tuxtla, Vera Cruz, Mexico (4800 feet). [Volcán Tuxtla, State of Veracruz]

Collected: 13 May 1894, by E. W. Nelson and E. A. Goldman (original no. 6253).

Comments: This is now Cryptotis mexicana nelsoni (Choate, 1970:234).

Blarina (Soriciscus) nigrescens, J. A. Allen, 8 November 1895:339.

Holotype: AMNH 9591/7952.

Type locality: San Isidro (San José), Costa Rica.

Collected: 5 September 1891, by George K. Cherrie.

Comments: This is now Cryptotis nigrescens.

Blarina obscura, C. H. Merriam, 31 December 1895:23.

Holotype: USNM 55634.

Type locality: Tulancingo, Hidalgo, Mexico (altitude, 8,500 feet).

Collected: 27 August 1893, by E. W. Nelson (original no. 5377).

Comments: This is now Cryptotis mexicana obscura (Choate, 1970:235).

Blarina olivaceus, J. A. Allen, 13 October 1908:669.

Holotype: AMNH 28356.

Type locality: San Rafael del Norte (altitude about 5000 feet), Nicaragua. [Jinotega Dept.]

Collected: by W. B. Richardson (original no. 41).

Comments: The tag on the type specimen indicates that it was identified as a female. However, shrews are notoriously difficult to sex because they lack external genitalia. This specimen has visibly well-developed, paired lateral glands, a characteristic almost exclusively found only in males. This suggests that the holotype of B. olivaceous was in reality a male.

The specific name should be olivacea in order to agree in gender with Cryptotis and Blarina.

This is a synonym of Cryptotis parva orophila (Choate, 1970:262).

Blarina (Soriciscus) orophila, J. A. Allen, 8 November 1895:340.

Holotype: AMNH 9640/9558.

Type locality: Volcan de Irazú. [Volcán Irazú; Cartago Prov.; Costa Rica]

Collected: February 1894 by G. K. Cherrie.

Comments: This is now Cryptotis parva orophila (Choate, 1970:262).

Blarina osgoodi, W. Stone, January 1914:16.

Holotype: ANSP 12732.

Type locality: Hacienda Garzon, Mt. Pichincha, 10,500 ft. altitude. [Cerro Pichincha; Pichincha Prov.; Ecuador]

Collected: 12 May 1911, by Samuel N. Rhodes.

Comments: This is a synonym of Cryptotis thomasi equatoris (Cabrera, 1958:47).

Blarina pergracilis, D. G. Elliot, February 1903:149.

Holotype: FMNH 8689 (Sanborn, 1947:217).

Type locality: Ocotlan, State of Jalisco, Mexico.

Collection: June 1901 by F. E. Lutz (original no. 161).

Comments: This is a synonym of Cryptotis parva berlandieri (Choate, 1970:260).

Blarina pyrrhonota, F. A. Jentinck, 1910:167.

Type locality: Surinam.

Comments: The type specimen first was mentioned by Jentinck (1888:131) as a new species, Blarina pyrrhonota, from Surinam, but was not described by him at that time, relegating it a nomen nudum. The name later was resurrected when Jentinck (1910) described the species. Cabrera (1958:47), without comment, placed this species as a synonym of Sorex surinamensis (see below), which he referred to the genus Cryptotis, the only genus of Insectivora presently known to occur in South America. After study of the holotype and its history, Husson (1963) concluded that the specimen probably is a common European shrew, Sorex araneus, and that the type locality was incorrect.

Blarina soricina, C. H. Merriam, 31 December 1895:22.

Holotype: USNM 50762.

Type locality: Tlalpam, Valley of Mexico (altitude, 7,600 feet). [10 mi S Mexico City; Distrito Federal; Mexico].

Collected: 5 December 1892, by E. W. Nelson (original no. 3989).

Comments: This is now Cryptotis parva soricina (Choate, 1970:267).

Blarina (Cryptotis) squamipes, J. A. Allen, 19 April 1912:93.

Holotype: AMNH 32378.

Type locality: crest of Western Andes (alt. 10,340 ft.), 40 miles west of Popayan, Cauca, Colombia. [Cordillera Occidental]

Collected:17 July 1911, by Leo E. Miller (original no. 286).

Comments: This is now Cryptotis squamipes (Tate, 1932:225).

Blarina thomasi, C. H. Merriam, 15 July 1897:227.

Holotype: BMNH

Type locality: Plains of Bogota, Colombia (on G. O. Child's estate near City of Bogota, alt. about 9000 feet). [Sabana de Bogota (Cabrera, 1958)], near Bogotá, Cundinamarca Dept.]

Collected: 14 November 1895.

Comments: This is now Cryptotis thomasi thomasi (Cabrera, 1958:48).

Blarina tropicalis, C. H. Merriam, 31 December 1895:21.

Lectotype: BMNH 7.1.1.33, designated by Choate (1970:268).

Type locality: Coban, Guatemala (altitude about 4,400

feet). [Alta Verapaz Dept.]

Collected: 1859 by L. Fraser and O. Salvin (Fraser's original no. 2778).

Comments: The name Corsira tropicalis was first used by Gray (1843b) for a shrew from Central America, but, because a description of the species was not provided, the name became a nomen nudum. Merriam (1895) noted that when Sorex micrurus Tomes (1861) was referred to the genus Blarina, the name micrurus became preoccupied by Galemys (Brachysorex) micrurus Pomel, 1848, a synonym of Blarina brevicauda (Say, 1823). In renaming S. micrurus, Merriam (1895:21) resurrected the specific epithet tropicalis as Blarina tropicalis. When he did this, however, Merriam did not designate a single holotype, but referred instead to the two specimens used by Tomes (1861) to describe Sorex micrurus. Oldfield Thomas selected and labeled a lectotype (Handley and Choate, 1970), but did not publish it. A lectotype was selected formally by Choate (1970:268). The correct name now is Cryptotis parva tropicalis (Choate 1970:268). See Handley and Choate (1969) for details of the nomenclatorial history.

Brachysorex harlani G. L. Duvernoy, 1842:40.

Type locality: New Harmony; Posey Co.; Indiana.

Comments: I have been unable to find either a copy of the original description or the location of the holotype of this species.

Hall (1981) considered this taxon to be a subspecies of C. parva. However, Hoffmeister (1989) treated C. parva harlani as a synonym of Cryptotis parva parva.

Corsira J. E. Gray, 1838:123.

Type species: Sorex araneus Linné.

Comments: Gray (1838) split the genus Sorex as it was then known into five separate genera, one of which was Corsira. This new genus included the new subgenus Blarina, which at that time incorporated the North American short-tailed shrews now in the genera Blarina and Cryptotis. Corsira is a junior synonym of Sorex.

Corsira tropicalis J. E. Gray, 1843:79.

Comments: Because this species was never described by Gray, it was relegated to the status of a nomen nudum. Merriam (1895) resurrected the name as Blarina tropicalis to replace the name Sorex micrurus Tomes (1861), which was preoccupied (see Handley and Choate, 1970).

+Cryptotis Pomel, 1848:249.

Type species: Sorex cinereus Bachman [= Cryptotis parva (Say)].

Comments: Cryptotis originally was named as a subspecies of Musaraneus Brisson (1762). It was later recognized as a subgenus of Blarina Gray (1838), replacing Soriciscus Coues (1877), over which it has precedence (Merriam, 1895). Cryptotis first appears to have been used formally as separate genus by Miller (1911).

+Cryptotis adamsi** - See Blarina adamsi.

+Cryptotis alticola - See Blarina alticola.

+Cryptotis avia, G. M. Allen, 12 February 1923:37.

Holotype: MCZ 20091.

Type locality: El Verjon, in the Andes east of Bogotá, Colombia. [Cundinamarca Dept.]

Collection: October 1922, by Brother Nicéforo Maria.

Cryptotis celatus, G. G. Goodwin, 28 September 1956:1.

Holotype: AMNH 145838.

Type locality: Las Cuevas; Santiago Lachiguiri; District of Tehuantepec; Oaxaca; México.

Collected: 15 December 1947 by Thomas MacDougall (original no. 623).

Comments: The specific name should be feminized to celata to agree in gender with Cryptotis.

This is a synonym of C. parva pueblensis (Choate, 1970:265).

+Cryptotis endersi, H. W. Setzer, 29 September 1950:300.

Holotype: ANSP 20955.

Type locality: Cylindro; Province of Chiriquí, Panama. [The type locality is in Bocas del Toro Province, rather than in Chiriquí Province (see Choate, 1970:286-287).

Collection: 24 July 1941, by R. K. Enders.

Cryptotis euryrhynchis, H. H. Genoways and J. R. Choate, 1 December 1967:203.

Holotype: KU 107143.

Type locality: Mexico: Volcán de Fuego (also called Volcán de Colima), 9800 ft, Jalisco.

Collected: 10 July 1966, by Percy L. Clifton (original no. 11059).

Comments: This is a synonym of C. alticola.

Cryptotis fossor - See Blarina fossor.

Cryptotis frontalis, G. S. Miller, 31 October 1911:222.

Holotype: USNM 123429.

Type locality: near the City of Tehuantepec, Mexico.

[State of Oaxaca]

Collected: by F. Sumichrast.

Comments: This is a synonym of C. goldmani.

+Cryptotis alticola - See Blarina alticola.

+Cryptotis goldmani - See Blarina mexicana goldmani.

+Cryptotis goodwini, H. T. Jackson, 27 April 1933:81.

Holotype: USNM 77074.

Type locality: Calel, 10,200 feet, Guatemala. [Quetzaltenango Dept.]

Collected: 13 January 1896, by E. W. Nelson and E. A. Goldman (original no. 9073).

+Cryptotis gracilis, G. S. Miller, 31 October 1911:221.

Holotype: USNM 12236/38471.

Type locality: at head of Lari River, near base of Pico Blanco, Talamanca, Costa Rica. Altitude about 6000 feet. [This portion of Talamanca is now Limón Province.]

Collected: by William M. Gabb.

+Cryptotis griseoventris, H. H. T. Jackson, 27 April 1933:80.

Holotype: USNM 75894.

Type locality: San Cristobal, altitude 9500 feet, State of Chiapas, Mexico.

Collected: 4 October 1895, by E. W. Nelson and E. A. Goldman (original no. 8545).

Cryptotis guerrerensis, H. H. T. Jackson, 27 April 1933:80.

Holotype: USNM 126895.

Type locality: Omilteme, altitude about 8000 feet, State of Guerrero, Mexico.

Collected: 17 May 1903, E. W. Nelson and E. A. Goldman (original no. 16429).

Comments: This is a synonym of C. goldmani.

+Cryptotis hondurensis, N. Woodman and R. M. Timm, 12 March 1992.

Holotype: KU 106941.

Type locality: Honduras; Francisco Morazan Prov.; 12 km WNW of El Zamorano; W slope of Cerro Uyuca (= Cerro Oyuca); 1680 m.

Collected: 5 July 1966, by William E. Duellman (original no. M1405).

+Cryptotis jacksoni, G. G. Goodwin, 10 December 1944:1.

Holotype: USNM 116649.

Type locality: Costa Rica: Volcan Irazu. [Volcán Irazú, Cartago Province]

Collected: 27 February 1902, by M. Cary (original no.

540/3549).

+Cryptotis kansasensis**, C. W. Hibbard, winter 1957:333.

Holotype: UMMP 34447.

Type locality: [University of Michigan] locality UM-K1-56, in the road bank north of the railroad along the west edge NW 1/4, sec. 24, T.30 S, R.5 W, one and three-fourths mile south and one mile east of Norwich, Kingman Co., Kansas.

Collected: 31 July 1956, by Charles W. Lane, Claude W. Hibbard, and party.

Age: early Pleistocene.

Stratigraphy: lower Pleistocene Meade Group.

+Cryptotis magna - See Blarina magna.

+Cryptotis mayensis - See Blarina mayensis.

+Cryptotis? meadensis**, C. W. Hibbard, January 1953.

Holotype: UMMP 27266.

Type locality: University of Michigan locality UM-K1-47, in Fox Canyon, sec. 35, T.34 S, R.30 W, Meade County, Kansas.

Collected: summer 1950, by Claude W. Hibbard and party.

Age: late Pliocene (early Blancan).

Stratigraphy: upper Pliocene Rexroad Fm., Rexroad fauna.

Comments: Although they noted that C. meadensis possesses some primitive characters relative to modern representatives of the genus, both Repenning (1967:40) and Choate (1970:291) referred this species to the genus Cryptotis.

Cryptotis medellinius, O. Thomas, September 1921:354.

Holotype: BMNH 21.7.1.9.

Type locality: Colombia: San Pedro, 30 km. north of Medellin. [30 km. north of Medellín; Antioquia Dept.]

Collection: December 1919 by Brother Nicéforo Maria.

Comments: Thomas (1921) refers to the collector by the French title, Frére Nicéforo Maria.

The correct spelling of the specific name is medellinia, in agreement with the feminine gender of Cryptotis (Woodman, in press).

This taxon is now C. thomasi medellinia (Cabrera, 1958:48).

+Cryptotis mera - See C. merus.

+Cryptotis merriami - See C. nigrescens merriami.

Cryptotis merus, E. A. Goldman, 20 September 1912:17.

Holotype: USNM 178976.

Type locality: near head of Rio Limon (altitude 4,500 feet), Mount Pirri, eastern Panama. [near head of Río Limón, Cerro Pirre, Darien Province]

Collected: 2 May 1912, by E. A. Goldman (original no. 21669).

Comments: The USNM catalog gives the date of collection as 16 April, but it is reported by Goldman (1912:17) as 2 May.

The correct spelling of the specific name is mera, in agreement with the feminine gender of Cryptotis (Woodman, in press).

Cryptotis mexicana goldmani - See Blarina mexicana goldmani.

Cryptotis mexicana machetes - See Blarina mexicana machetes.

Cryptotis mexicana madrea, G. G. Goodwin, 28 June 1954b:1.

Holotype: AMNH 147901.

Type locality: Rancho de Cielo, 3500 feet elevation, 5 miles northwest of Gómez Farías, Sierra Madre Oriental, Tamaulipas, Mexico.

Collected: 7 July 1951, by Marian Martin (original no. 325).

Comments: This taxon is a synonym of C. mexicana obscura (Choate, 1970:235).

+Cryptotis mexicana mexicana - See Blarina (Soriciscus) mexicana.

+Cryptotis mexicana nelsoni - See Blarina nelsoni.

+Cryptotis mexicana obscura - See Blarina obscura.

+Cryptotis mexicana peregrina - See Blarina mexicana peregrina.

Cryptotis micrura - See Sorex micrurus.

+Cryptotis montivaga - See Blarina montivaga.

Cryptotis nelsoni - See Blarina nelsoni.

+Cryptotis nigrescens - See Blarina (Soriciscus) nigrescens.

+Cryptotis nigrescens merriami, J. R. Choate, 30 December 1970:277.

Holotype: USNM 77050.

Type locality: Jacaltenango, 5400 ft., Huehuetenango, Guatemala.

Collected: 21 December 1895, by E. W. Nelson and E. A. Goldman (original no. 8846).

Comments: This is now C. merriami.

Cryptotis obscura - See Blarina obscura.

Cryptotis olivacea - See Blarina olivaceus.

Cryptotis orophila - See Blarina (Soriciscus) orophila.

+Cryptotis parva berlandieri - See Blarina berlandieri.

+Cryptotis parva elasson, B. P. Bole, Jr., and P. N. Moulthrop, 11 September 1942:97.

Holotype: CMNH 14025.

Type locality: Bettsville, Seneca County, Ohio.

Collected: 1 February 1939, by Winston C. Jesseman.

+Cryptotis parva floridana - See Blarina floridana.

Cryptotis parva harlani - See Brachysorex harlani.

+Cryptotis parva orophila - See Blarina (Soriciscus) orophila.

+Cryptotis parva parva - See Sorex parvus.

+Cryptotis parva pueblensis - See Cryptotis pergracilis pueblensis.

+Cryptotis parva soricina - See Blarina soricina.

+Cryptotis parva tropicalis - See Blarina tropicalis.

Cryptotis pergracilis macer, G. S. Miller, 31 October 1911:223.

Holotype: USNM 15565/38494.

Type locality: near Guanajuato City, Mexico. [State of Guanajuato]

Collected: by A. Dugés (original no. 103).

Comments: This is a synonym of C. parva berlandieri (Choate, 1970:260).

The subspecific name should be corrected to macera to agree with the feminine gender of Cryptotis.

Cryptotis pergracilis macra

Comments: This misspelling of C. p. macera may have been an attempt to feminize C. p. macer by Miller and Kellogg (1955:39).

Cryptotis pergracilis nayaritensis, H. H. T. Jackson, 27 April 1933:79.

Holotype: USNM 88015.

Type locality: Tepic, altitude 3000 feet, State of Nayarit, Mexico.

Collected: 13 April 1897, by E. W. Nelson and E. A. Goldman (original no. 10902).

Comments: This is a synonym of C. parva berlandieri (Choate, 1970:260).

Cryptotis pergracilis pergracilis - See Blarina pergracilis.

Cryptotis pergracilis pueblensis, H. H. T. Jackson, 27 April 1933:79.

Holotype: USNM 92720.

Type locality: Huauchinango, altitude 5000 feet, State of Puebla, Mexico.

Collected: 6 January 1898, by E. A. Goldman (original no. 12014).

Comments: This is now C. parva pueblensis (Choate, 1970:264).

Cryptotis soricina - See Blarina soricina.

+Cryptotis squamipes - See Blarina (Cryptotis) squamipes.

Cryptotis tersus, G. G. Goodwin, 28 June 1954a:1.

Holotype: AMNH 164695.

Type locality: Santa Clara, 4200 feet elevation, on the Pan American Highway, 15 miles from the border of Costa Rica, Chiriquí Province, Republic of Panama.

Collected: January 1953, by Frank A. Hartman.

Comments: This is a synonym of C. nigrescens.

The specific name should be tersa to agree in gender with the generic name.

+Cryptotis thomasi equatoris - See Blarina equatoris.

+Cryptotis thomasi medellinia - See Cryptotis medellinius.

Cryptotis thomasi medellinius - See Cryptotis medellinius.

+Cryptotis thomasi meridensis - See Blarina meridensis.

+Cryptotis thomasi thomasi - See Blarina (Cryptotis) thomasi.

Cryptotis zeteki, H. W. Setzer, 29 September 1950:299.

Holotype: USNM 290466.

Type locality: Cerro Punta (8°42' N, 82°48' W), 6,500 feet, Chiriquí Province, Republic of Panama.

Collection: April 1949, by Eric Graetz; presented to the U.S. National Museum by James Zetek.

Comments: This is a synonym of C. nigrescens.

Musaraneus M. J. Brisson, 1762:126.

Type species: Musaraneus [no specific epithet].

Comments: Cryptotis Pomel (1848) first appeared as a section (subgenus) of the genus Musaraneus. Musaraneus was first introduced in Brisson's (1756:178) Regnum Animale in Classes IX Distributum. Because the International Code of Zoological

Nomenclature (Ride et al., 1985) states that a scientific name must have been published after the year 1757 (Articles 3, 11) to be available, authors who refer to Musaraneus usually give Brisson's (1762) second edition of Regnum Animale as the original description (e.g., Hall, 1981:25, lists Musaraneus as a synonym for Sorex). However, because Brisson did not apply the principles of binomial nomenclature throughout his work, his names are considered unavailable except where made available by other authors at later dates (Hopwood, 1947), or as individually approved by the International Commission on Zoological Nomenclature (e.g., Hemming, 1957).

Musaraneus brasiliensis, M. J. Brisson, 1762:126.

Type locality: Brazil.

Comments: Like the genus to which it belongs, M. brasiliensis is unavailable because Brisson (1762) included many non-binomial names in his work. The species is of interest, however, because the genus Musaraneus clearly was regarded by Brisson (1756, 1762) and Pomel (1848) to include what are now considered to be Insectivora, and the type of M. brasiliensis hailed from Brazil, where Insectivora are unknown. Based on the original description of

the species, it is clear that Brisson (1762) was describing the South American didelphid marsupial Monodelphis americana.

Notiosorex (Xenosorex) phillipsii, W. J. Schaldach, Jr., October 1966:289.

Holotype: IBUNAM 8445.

Type locality: Río Molino, 3 kilometers S.W. San Miguel Suchixtepec, altitude 2250 meters, southern Oaxaca, México.

Collected: 18 December 1964, by W. J. Schaldach, Jr. (original no. 13278).

Comments: This is a synonym of Cryptotis mexicana peregrina (Choate, 1969:475).

Sorex, C. von Linné, 1758:53.

Type species: Sorex araneus.

Comments: This was the first soricid genus named, and at one time it included New World species now referred to Cryptotis and Blarina.

Sorex micrurus, R. F. Tomes, 25 June 1861:279.

Lectotype: BMNH 7.1.1.33 (lectotype infromally designated by O. Thomas - see Handley and Choate, 1970).

Type locality: Dueñas, Guatemala. [Type locality corrected to Cobán by Alston (1877), see Handley and

Choate(1970); this is in Alta Verapaz Department]

Collection: by Osbert Salvin.

Comments: The nomenclatorial history of the name micrurus is complicated, and it was sorted out by Handley and Choate (1970).

Paired with the feminine genus Cryptotis, the specific name would agree in gender and thus be micrura (Woodman, in press).

This is a synonym of C. parva tropicalis (Choate, 1970).

Sorex parvus, T. Say, 1823:163.

Type locality: Engineer Cantonment. [This is near Blair; Washington Co.; Nebraska. James (1823) describes the location of the encampment as on the west bank of the Missouri River, about one half mile above Fort Lisa, 5 miles below Council Bluff, and 3 miles above mouth of Boyer River.]

Collected: between 24 September - 31 October, 1819.

Comments: Say did not designate a holotype when he described S. parvus and none is known to be present in any of the major collections in the United States.

The taxon is now Cryptotis parva parva (Hall and Kelson, 1959:58).

Sorex surinamensis, J. F. Gmelin, 1789:114.

Type locality: Surinam.

Comments: Based on Gemelin's original description of S. surinamensis, Tate (1932:223) thought that this taxon represented a real soricid and that it was possibly the holotype of Blarina pyrrhonota Jentinck (1910). However, Husson (1963:35), who was the first to study the type of B. pyrrhonota since Jentinck, stated that there is no evidence to support this, although the original label has been lost. Thomas (1888:357) and Cabrera (1919:42) believed that Gmelin's description represented a marsupial mouse opossum, Monodelphis brevicaudata. As far as I can determine, the holotype of S. surinamensis is lost, and no one has studied it since the species was first described.

Soriciscus, E. Coues, 15 May 1877:649.

Type species: "Sorex parvus Say or S. cinereus Bachman" [= Cryptotis parva (Say)].

Comments: Soriciscus was named as a subgenus of Blarina, but was shown by Merriam (1895:6) to be antedated by Cryptotis Pomel (1848).

Sorieiscus

Comments: This is Elliot's (1901:382) misspelling of Soriciscus.

Xenosorex W. J. Schaldach, October 1966:289.

Type species: Notiosorex phillipsii Schaldach.

Comments: Xenosorex was described as a subgenus of Notiosorex, but the type species was shown to be a synonym of Cryptotis mexicana peregrina (Choate, 1969:475).

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[The year 1857 is listed on the frontispiece of this report, but E. R. Hall's copy, previously owned by H. T. Martin, is a handwritten note that the first

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[Charles von Linné is normally given as the author of this work, particularly in libraries, because the book is primarily a translation of Gmelin's (1789) revision of Linné's (1758) famous Systemae Naturae. However, Kerr's translation includes some important additions, the most notable being the first assignment of Latin binomial names to a number of mammalian species. Because these species now bear

Kerr's name (e.g., Didelphis virginiana Kerr, 1792), it is important that the book be listed under his name so that it can be located readily. See Thomas (1879) for a list of mammalian species named in Kerr's book. The work consists of two parts in one volume. Part I, on pages 1-432, is the Mammalia, and Part II, on pages 469-644, is a portion of Aves. Pages 433-468 were reserved to complete the Systematic Catalogue of Birds, but this was never finished.]

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[This is usually referenced with S. H. Long as the

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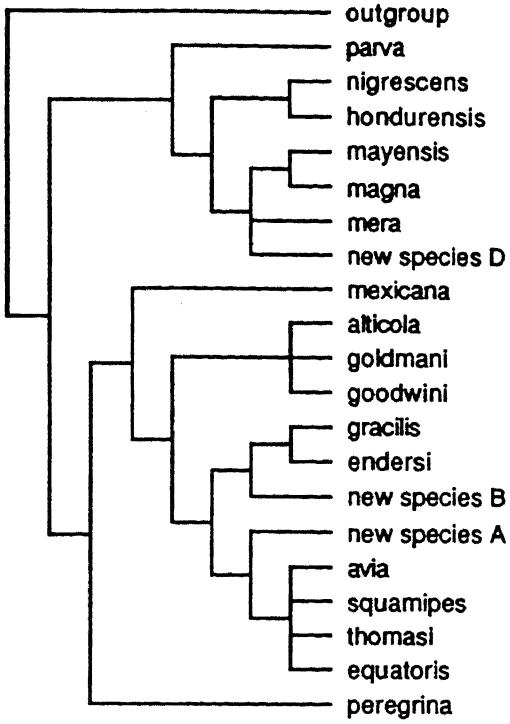
APPENDIX II

MINIMUM LENGTH TREES FROM PHYLOGENETIC ANALYSIS OF THE GENUS *CRYPTOTIS*

On the following pages are presented the 87 most-parsimonious trees resulting from phylogenetic analysis of a data matrix consisting of 19 transformation series containing 44 characters. These trees each have a consistency index = 0.583, rescaled consistency index = 0.473, homoplasy index = 0.521, and retention index = 0.811.

Among the terminal taxa on the trees, *C. mayensis* includes *C. merriami*, *C. goodwini* includes *C. griseoventris* and *Cryptotis* "C", and *C. gracilis* includes *C. jacksoni*.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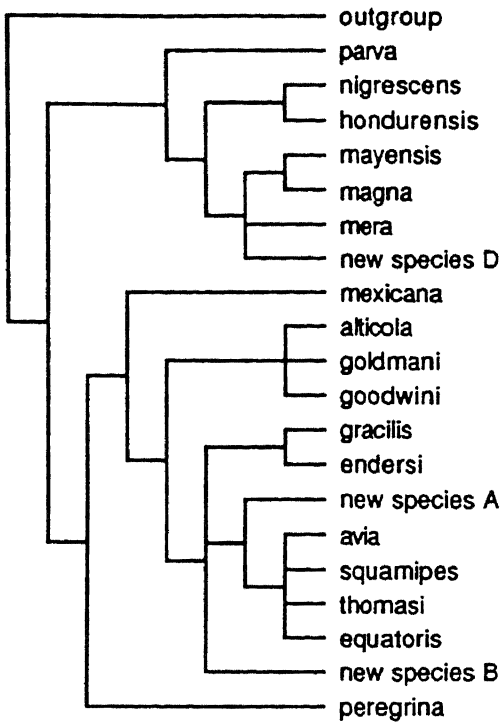
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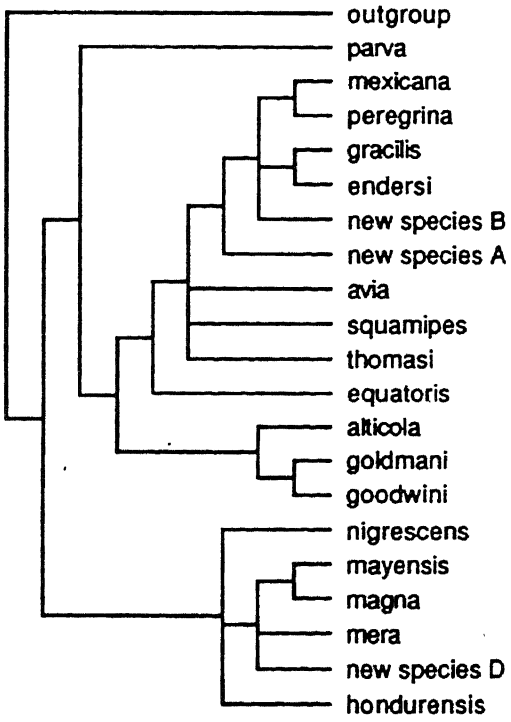
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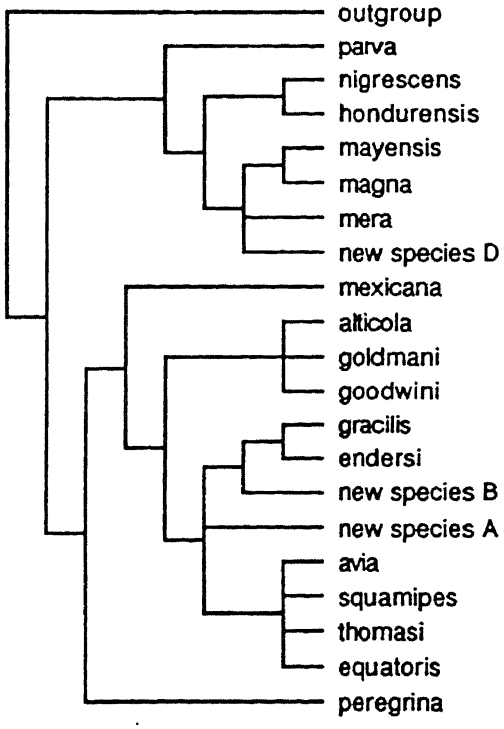
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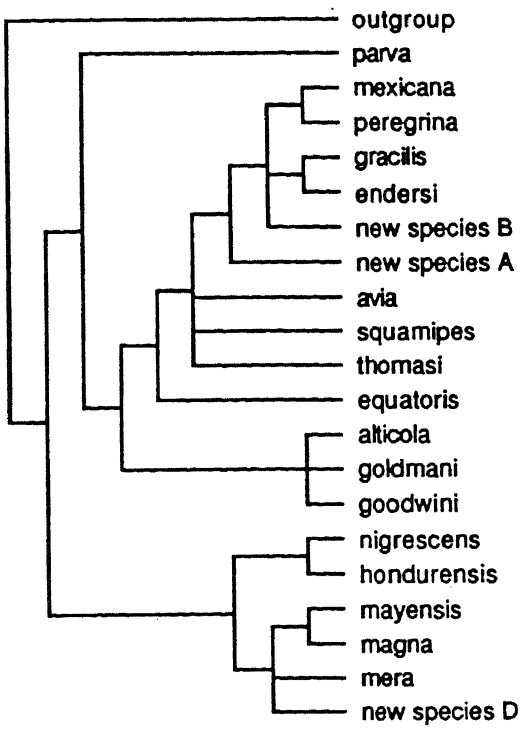
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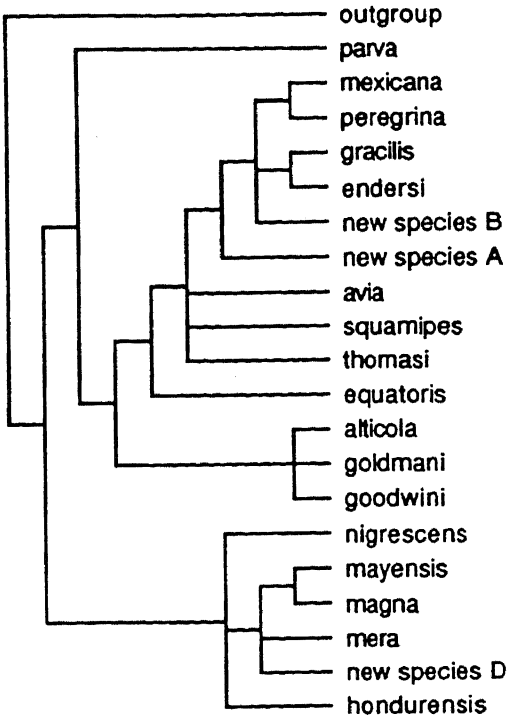
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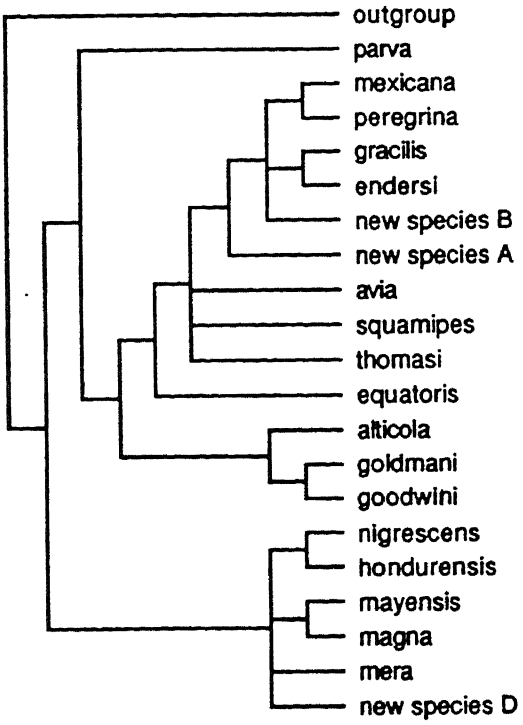
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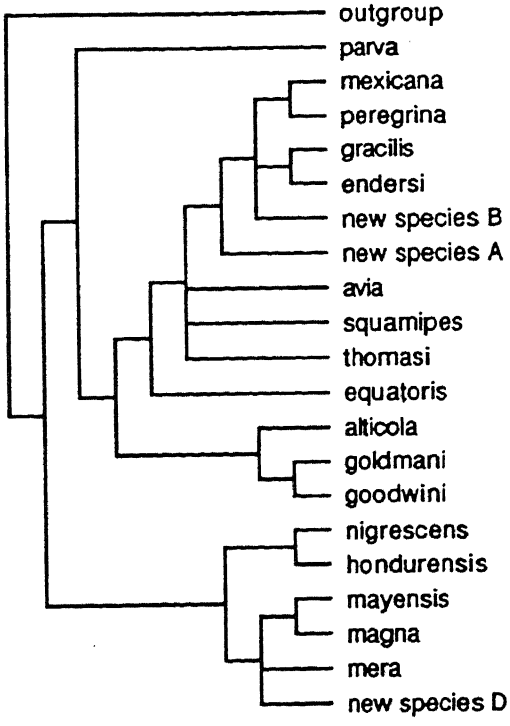
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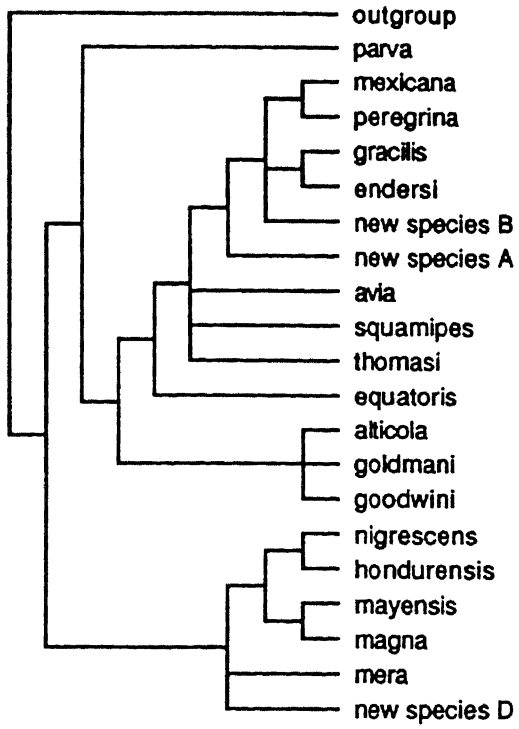
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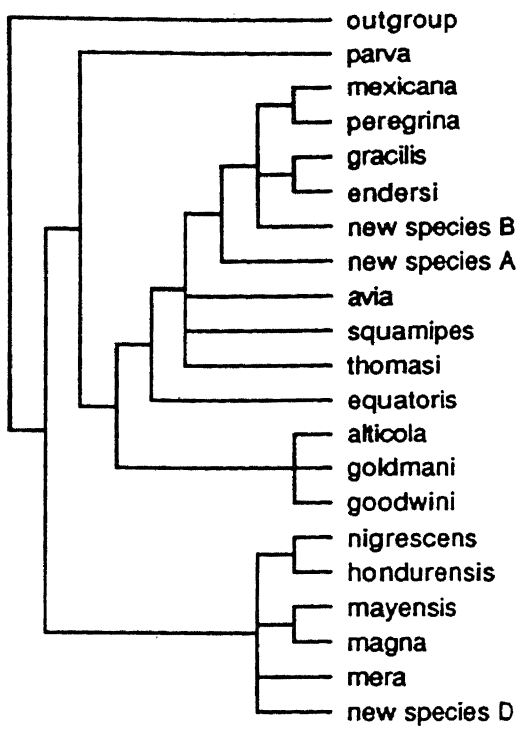
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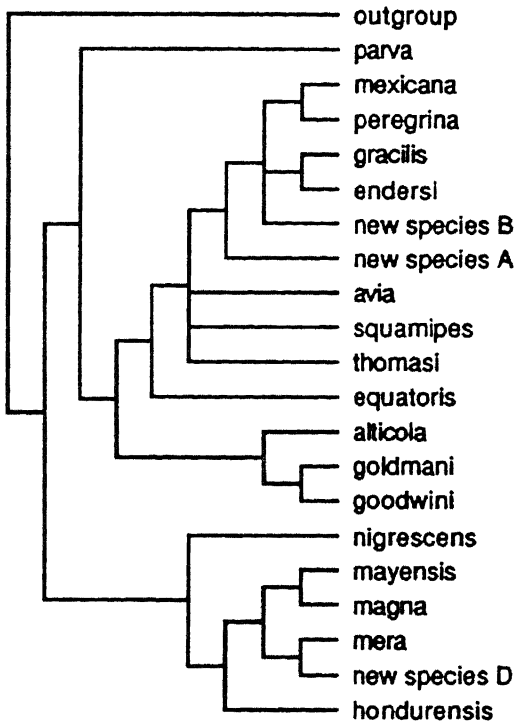
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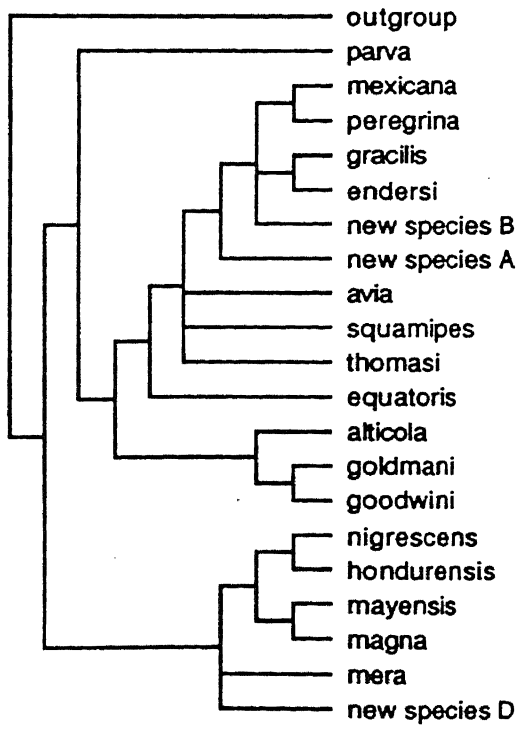
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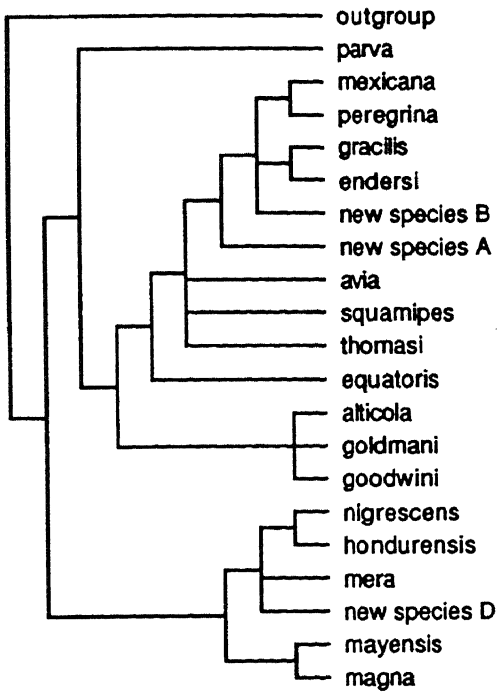
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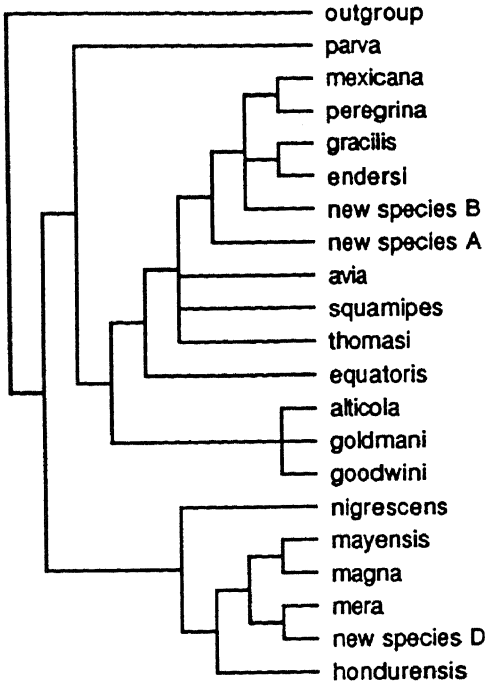
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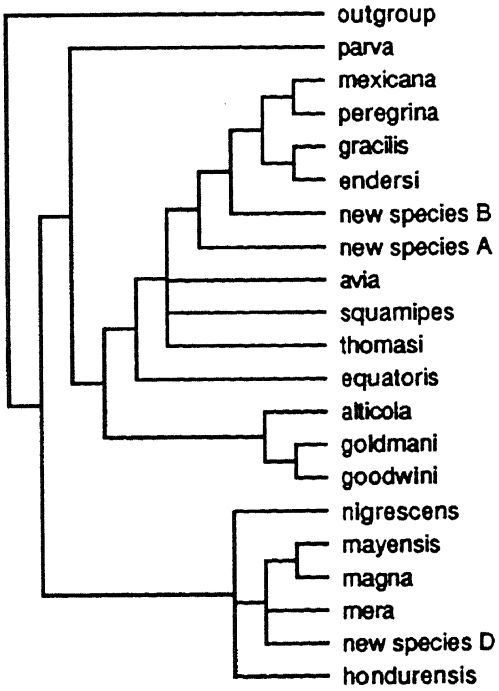
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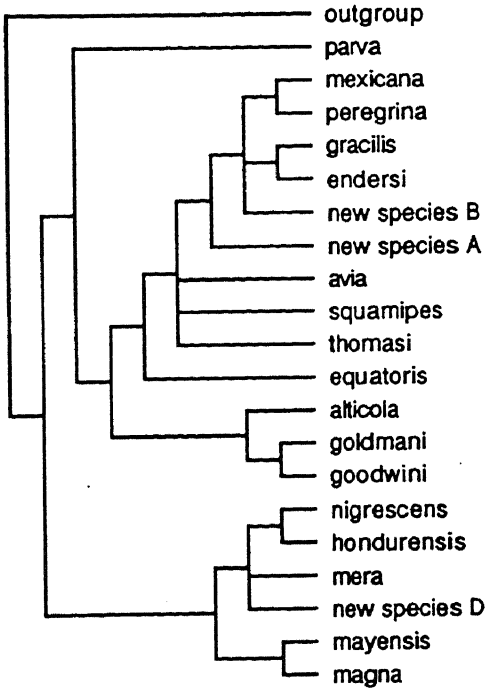
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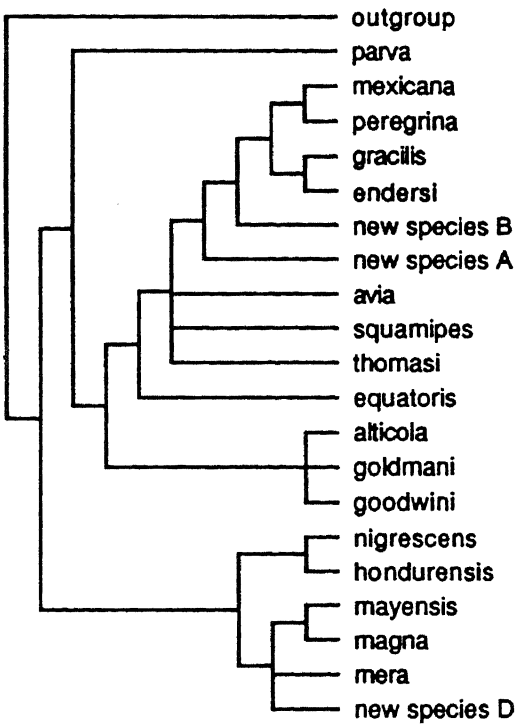
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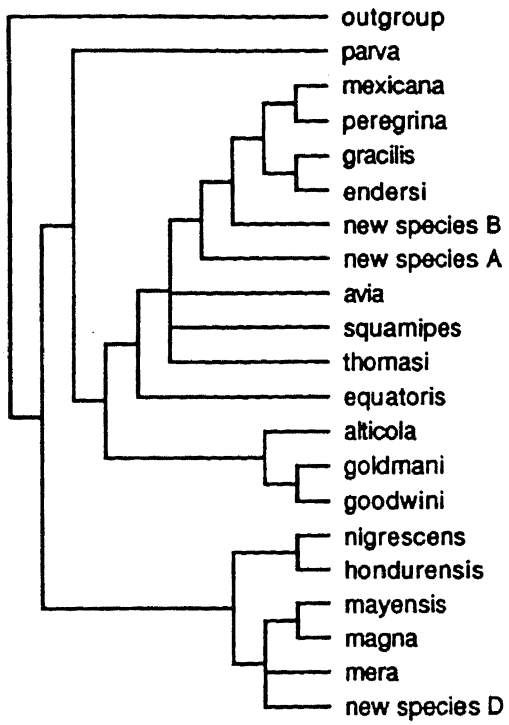
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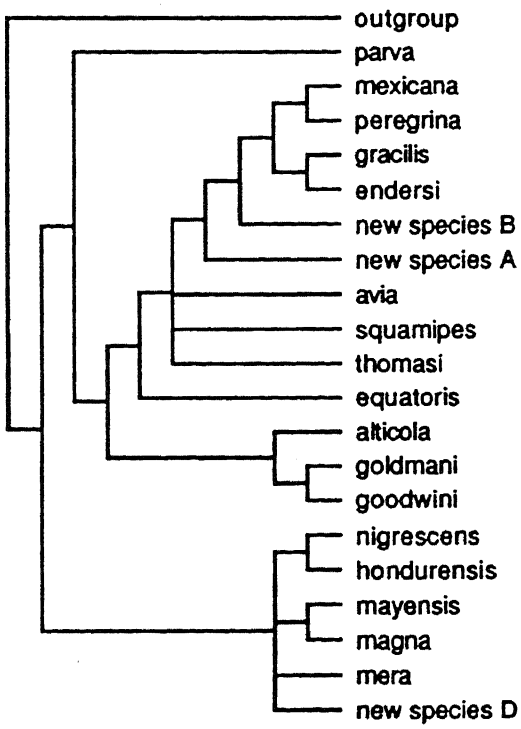
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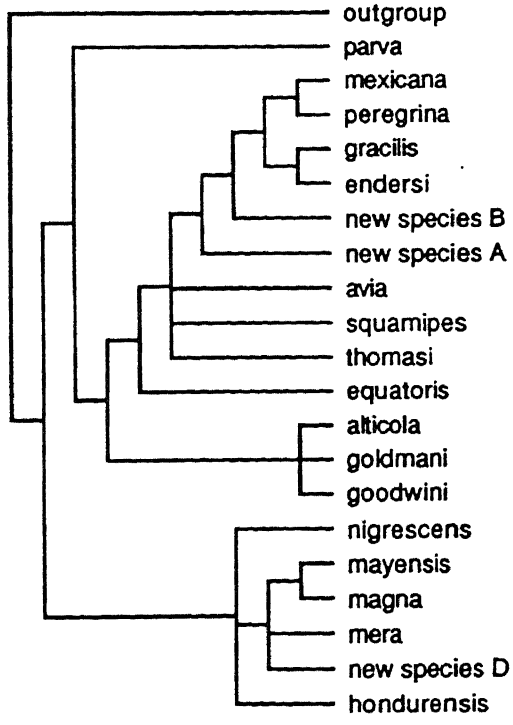
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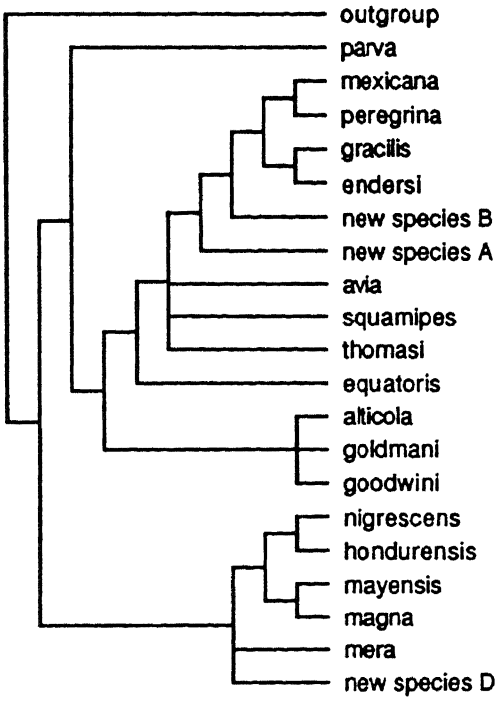
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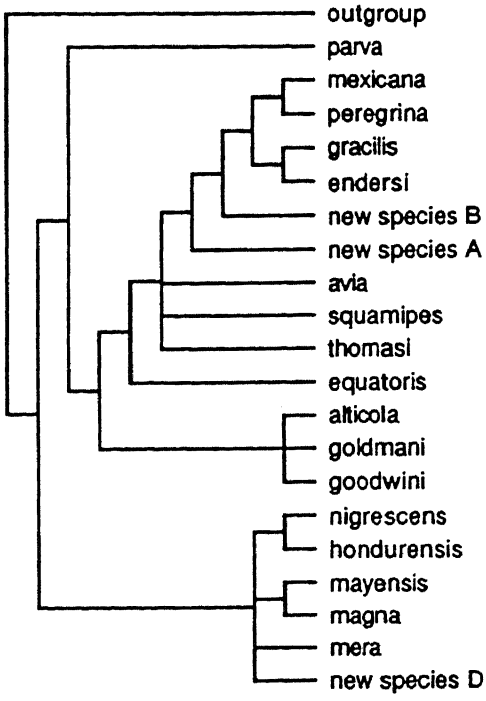
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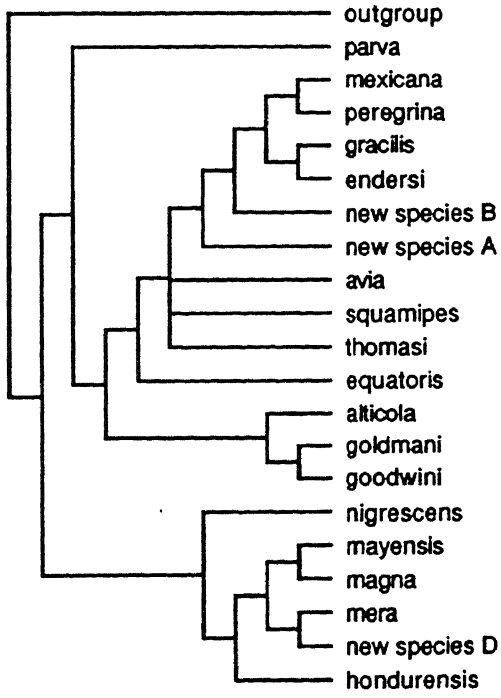
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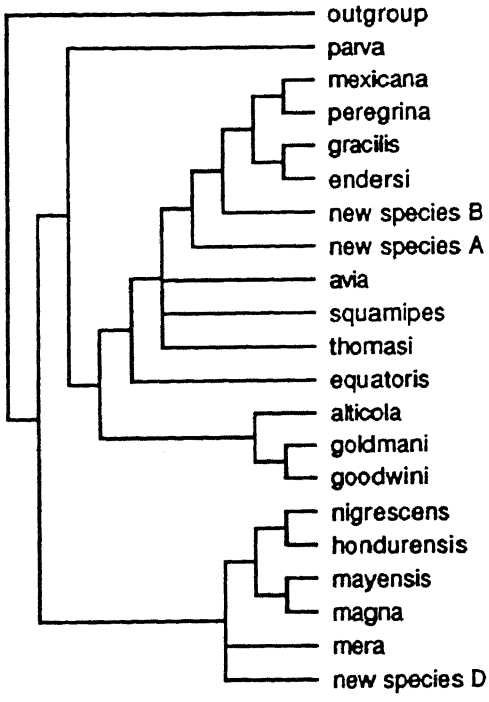
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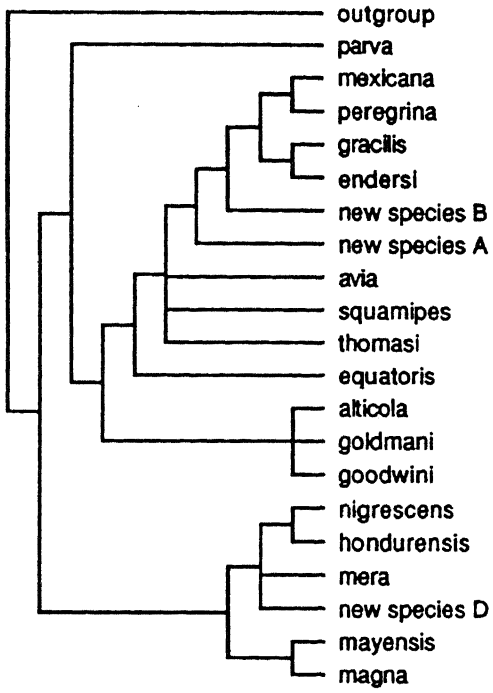
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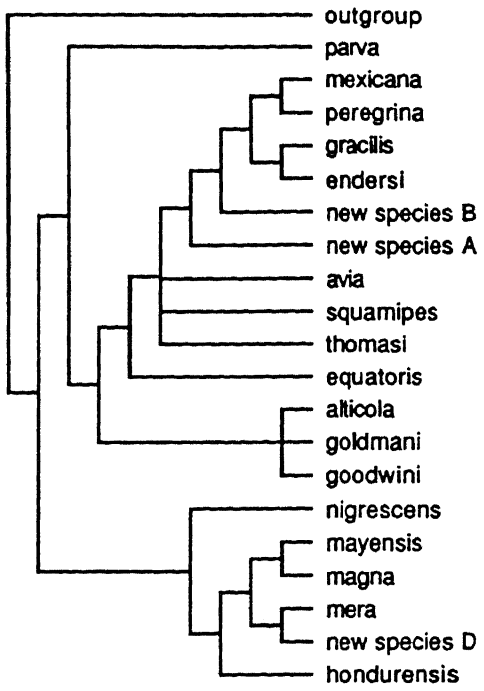
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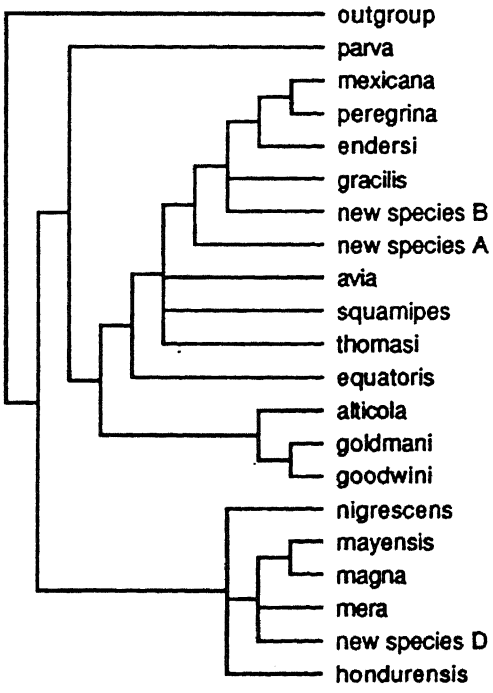
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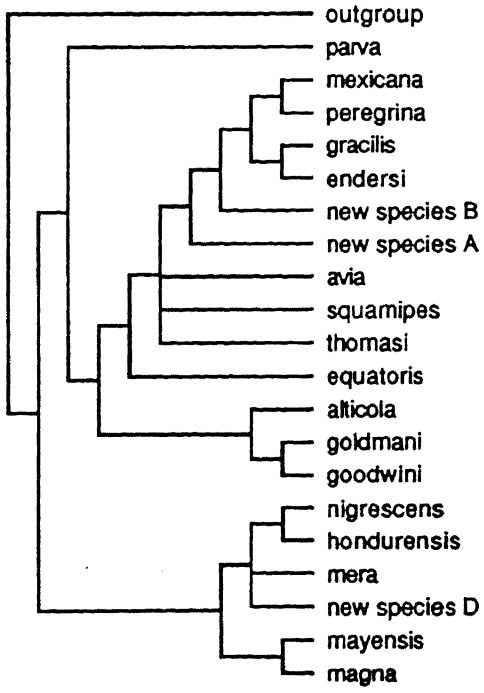
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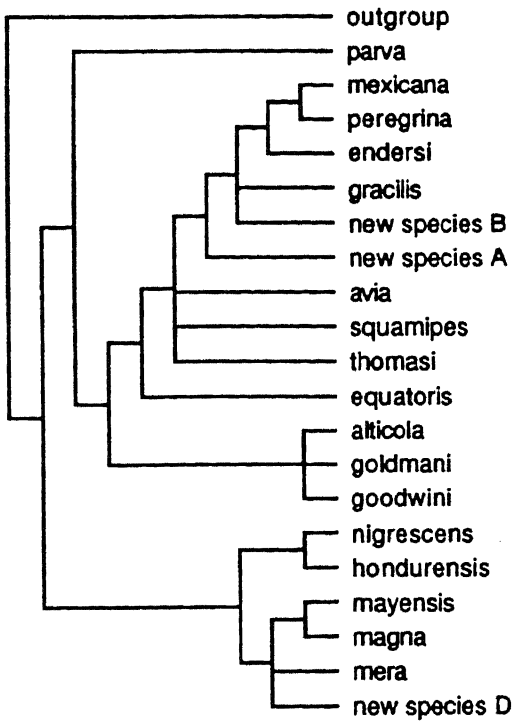
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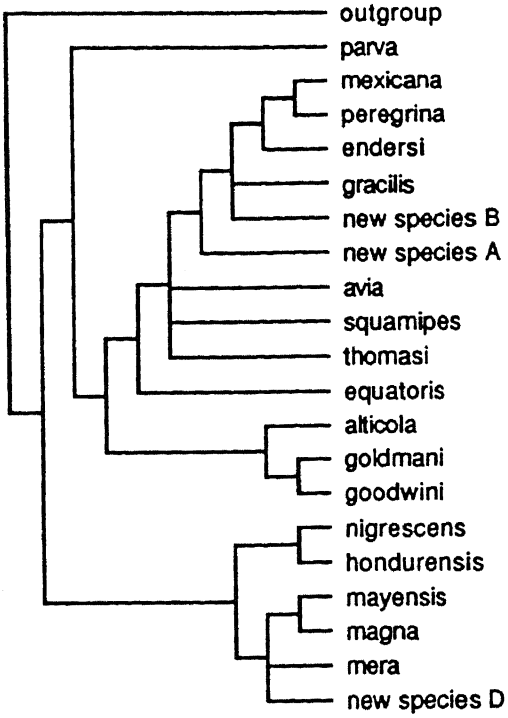
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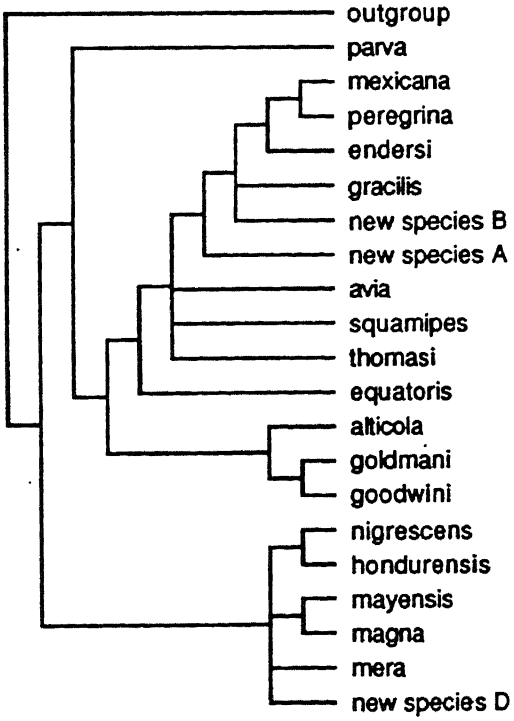
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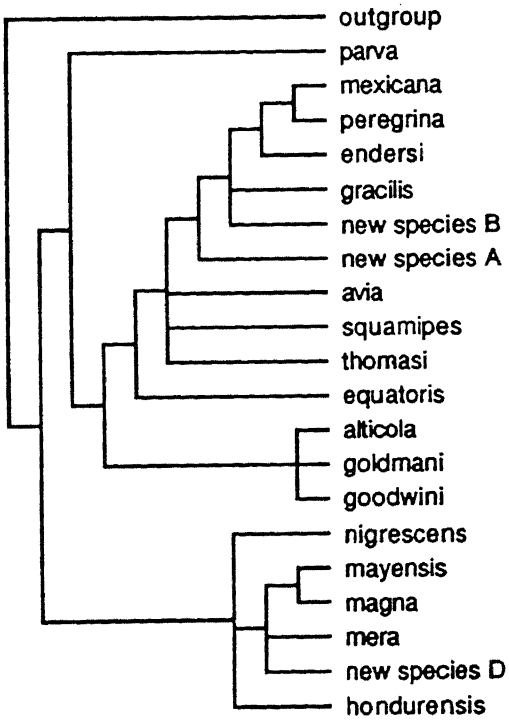
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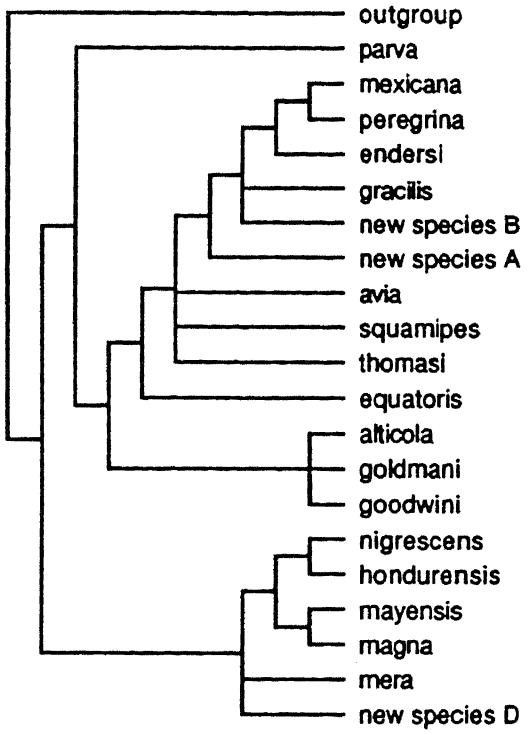
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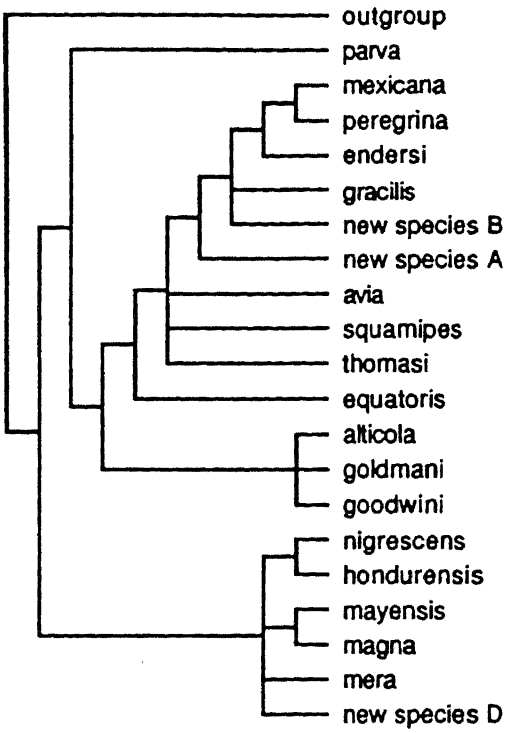
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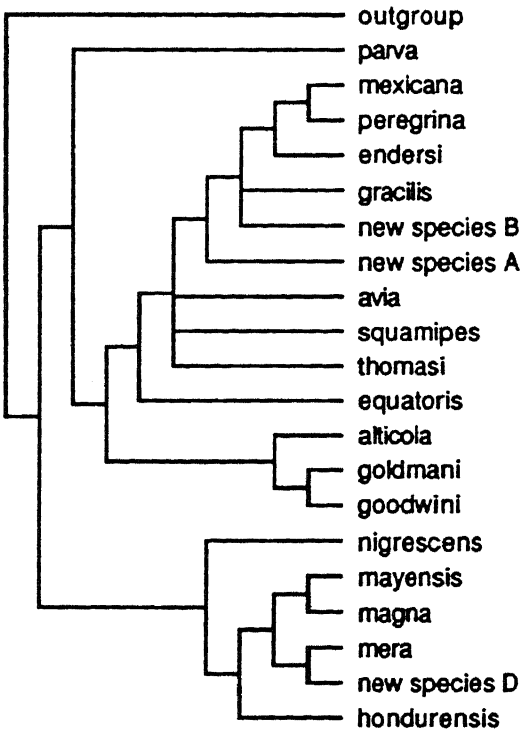
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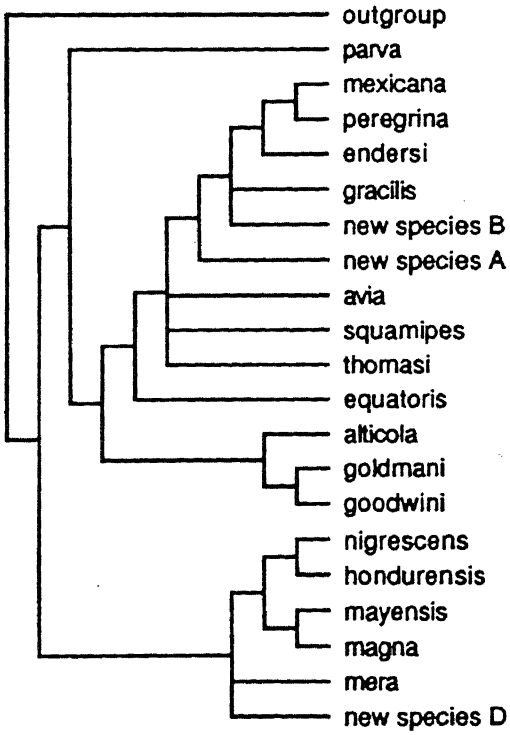
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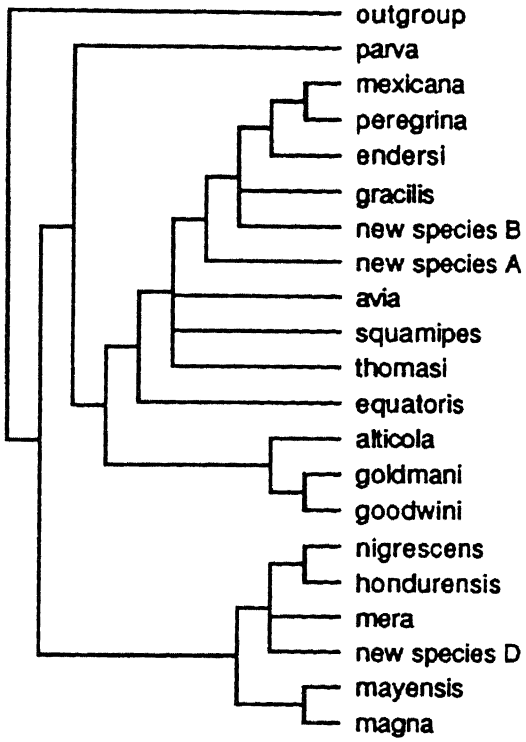
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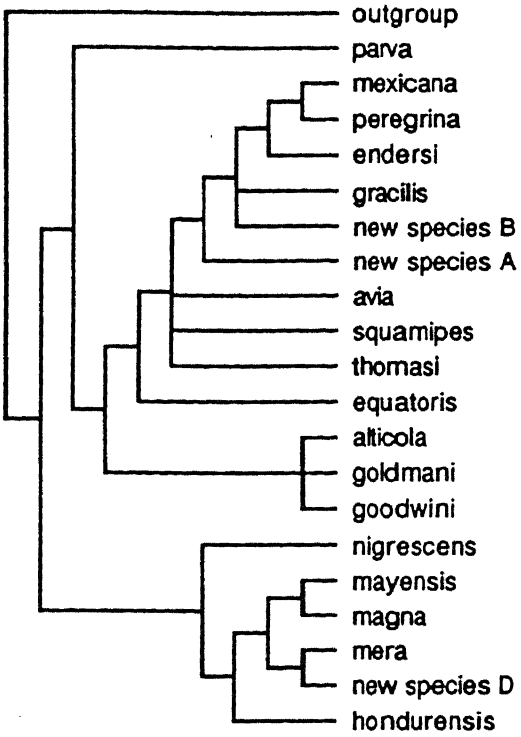
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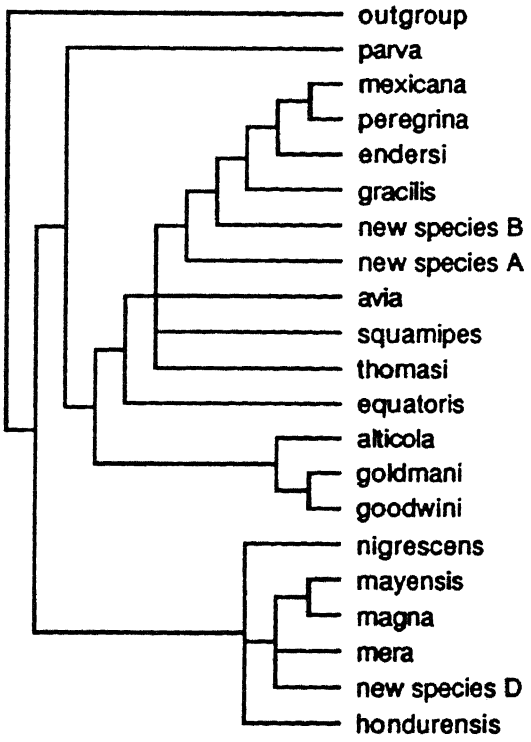
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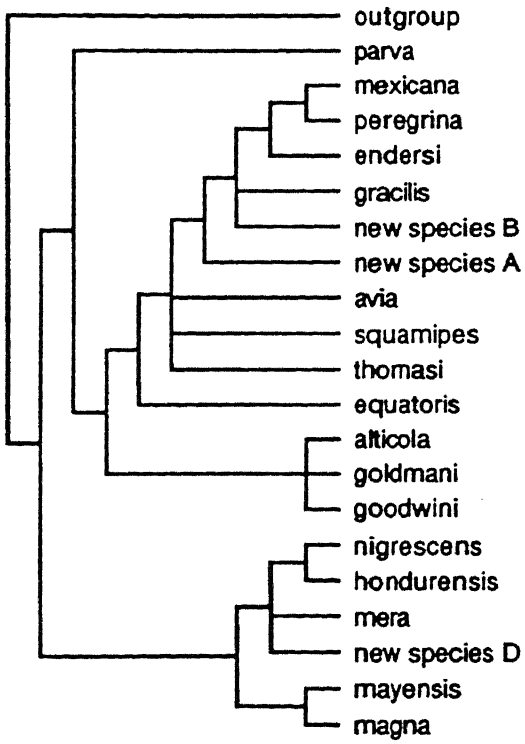
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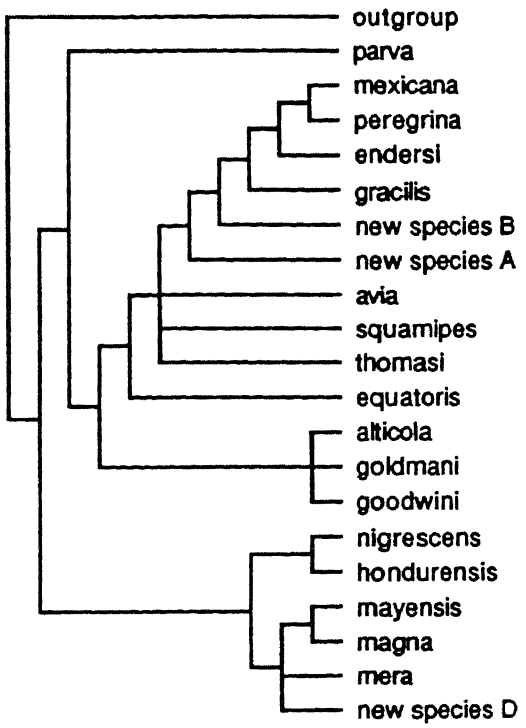
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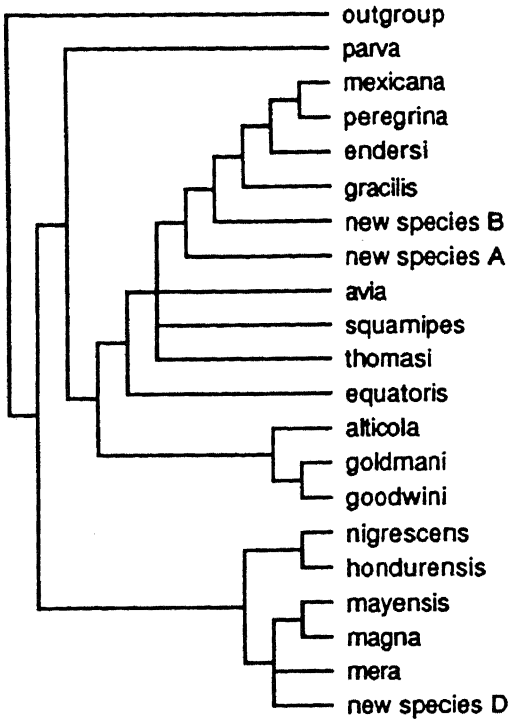
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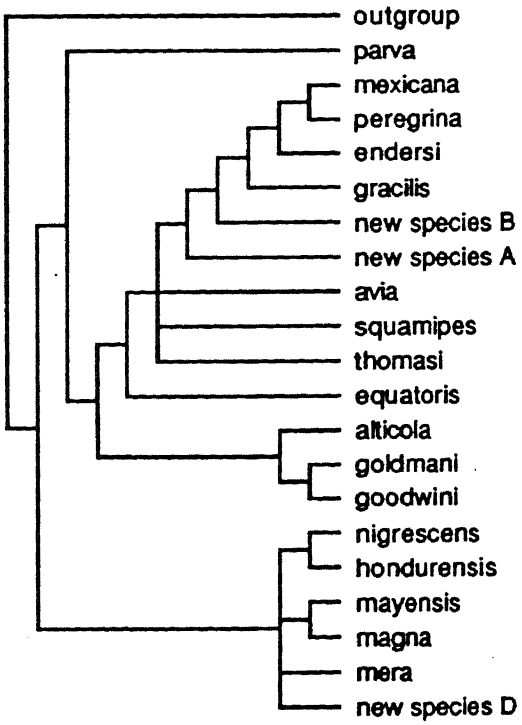
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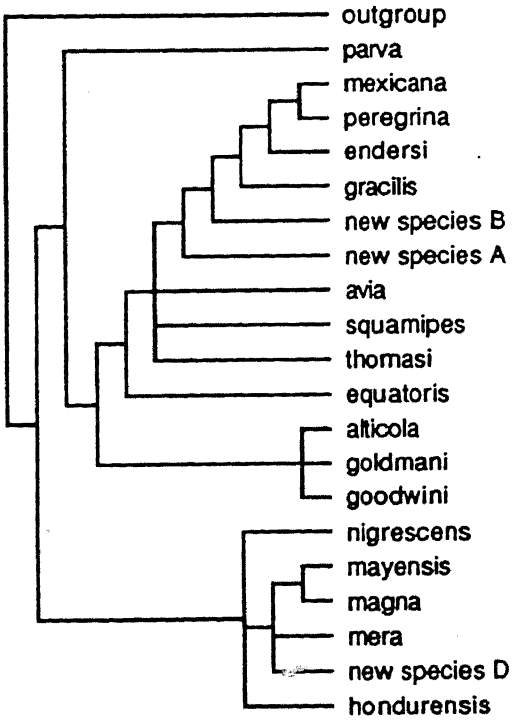
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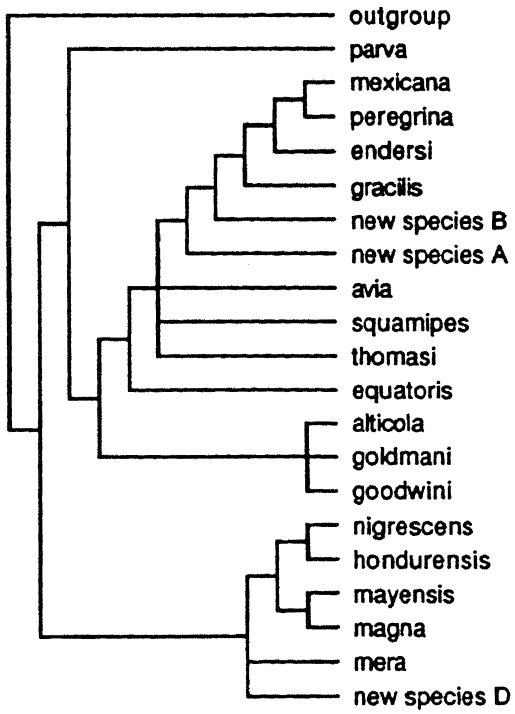
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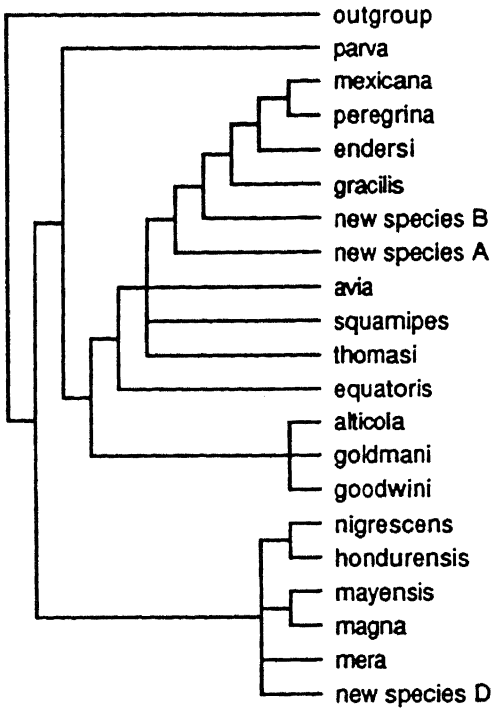
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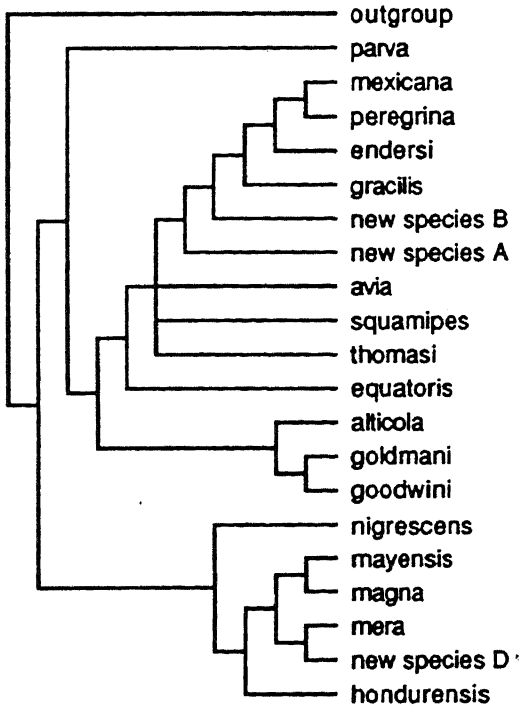
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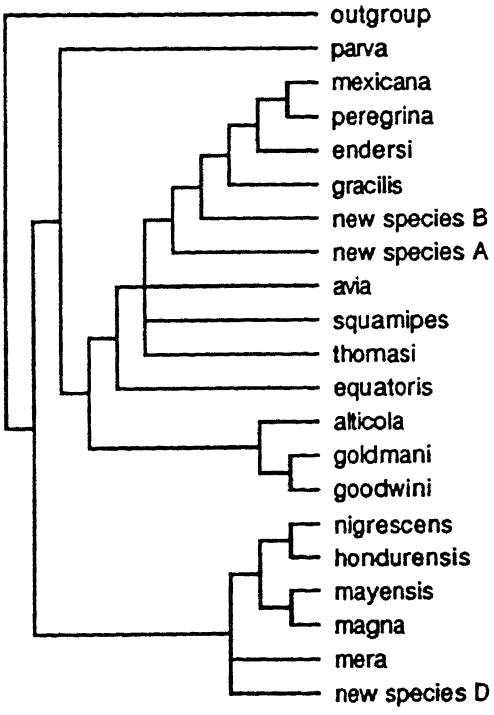
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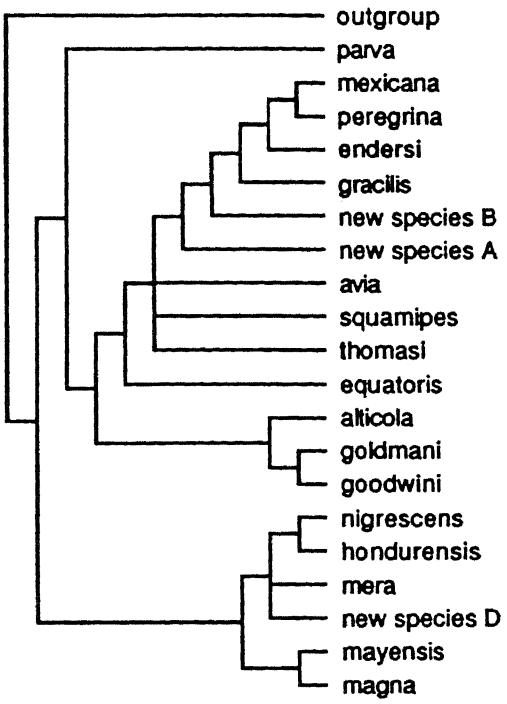
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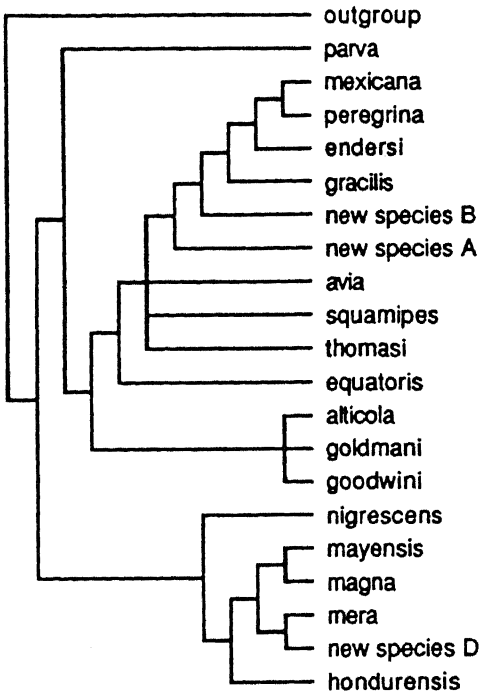
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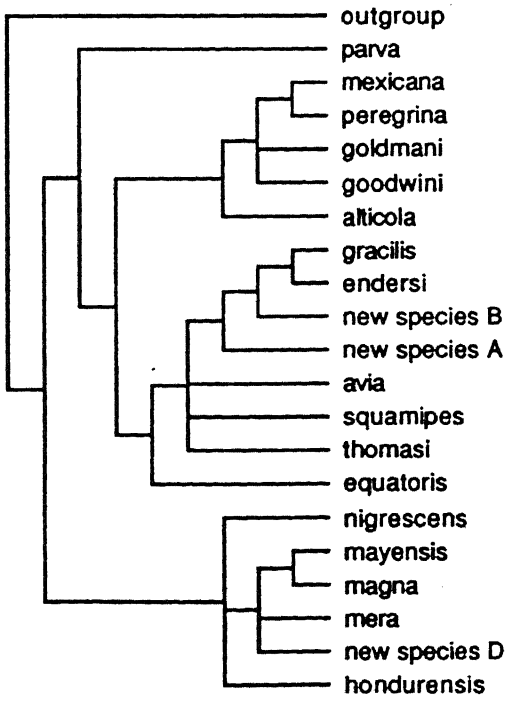
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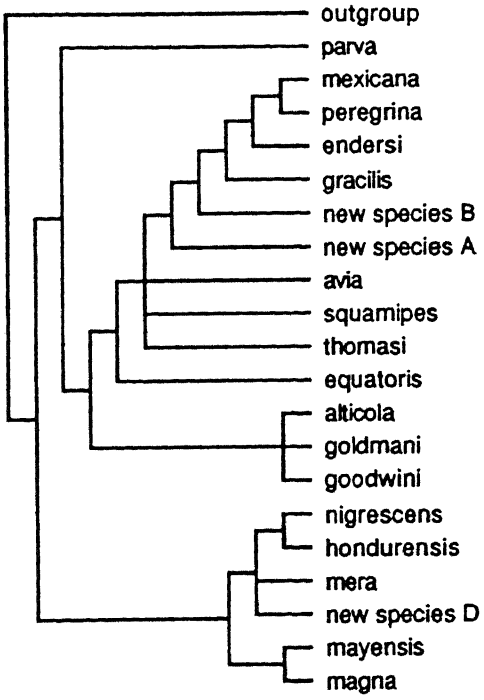
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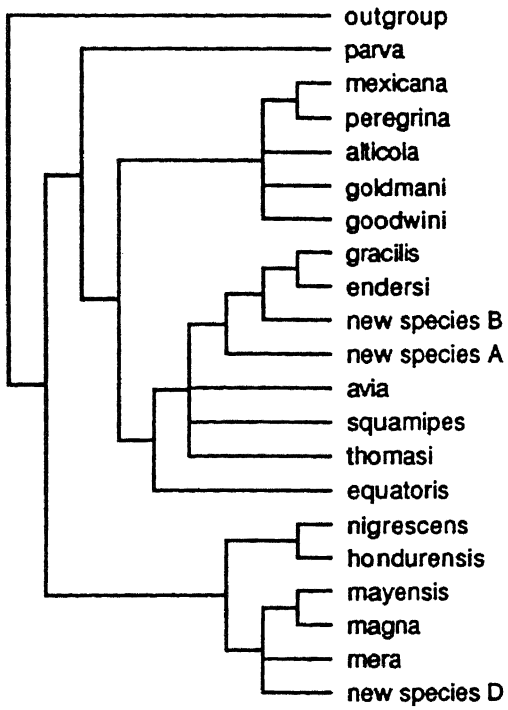
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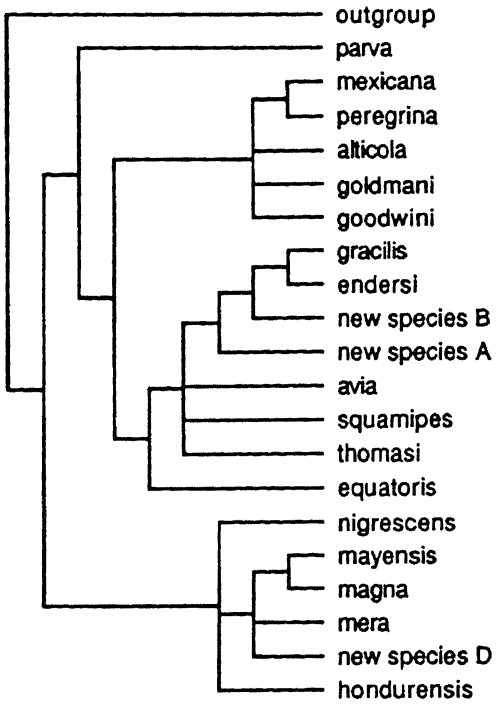
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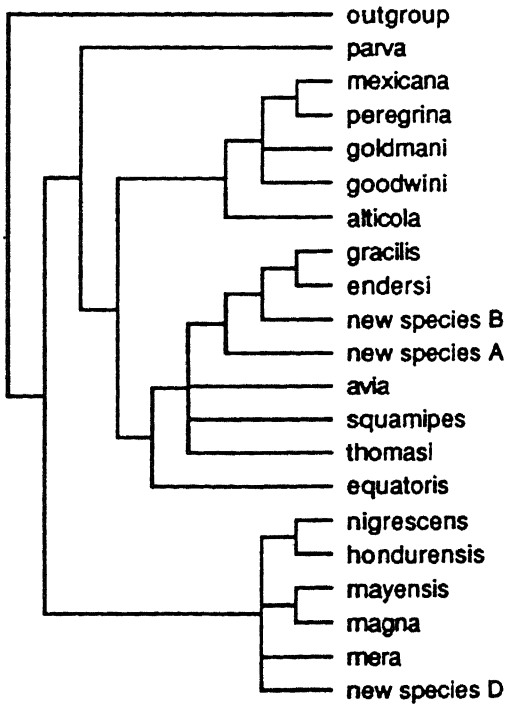
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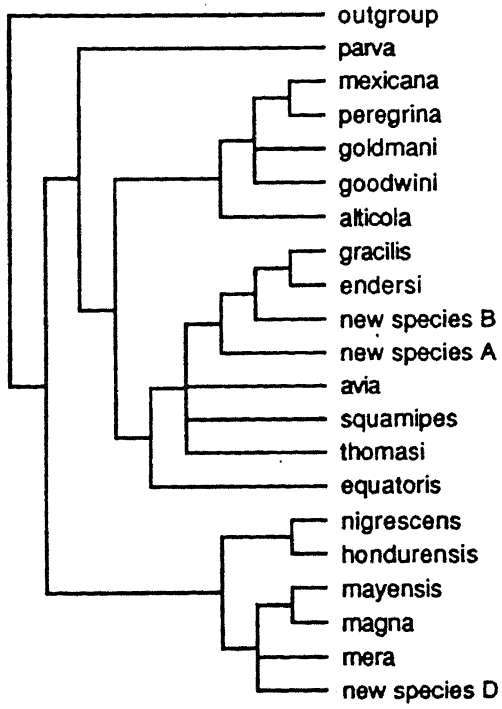
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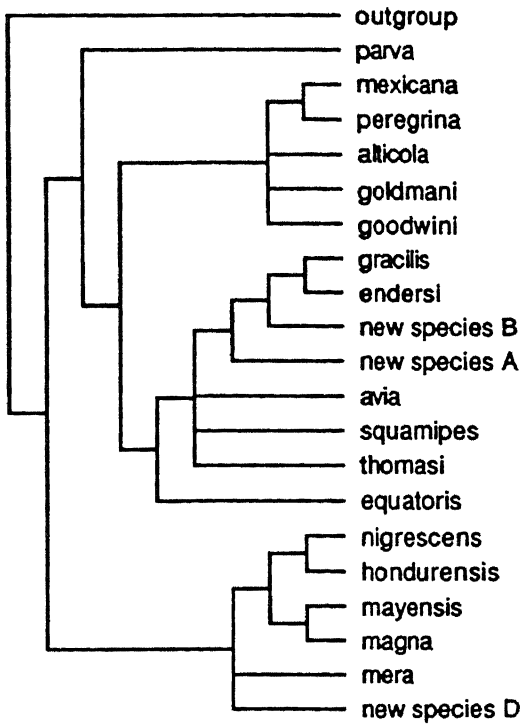
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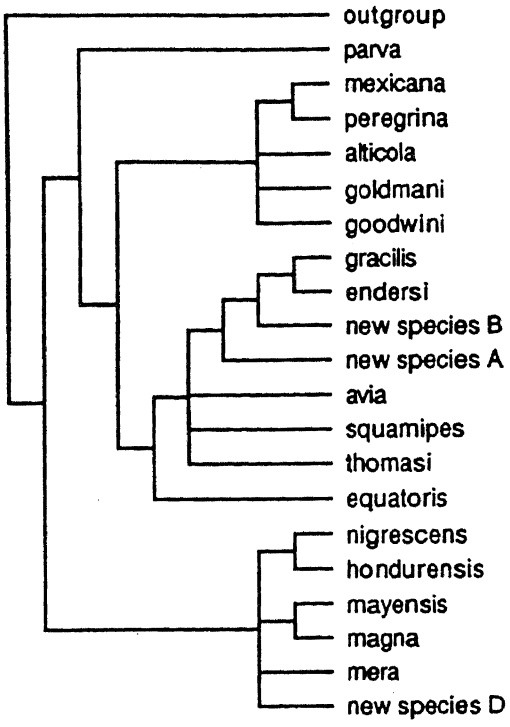
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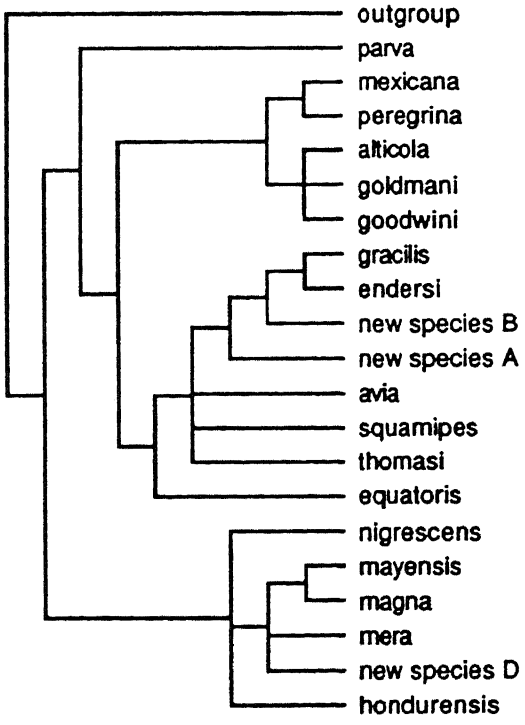
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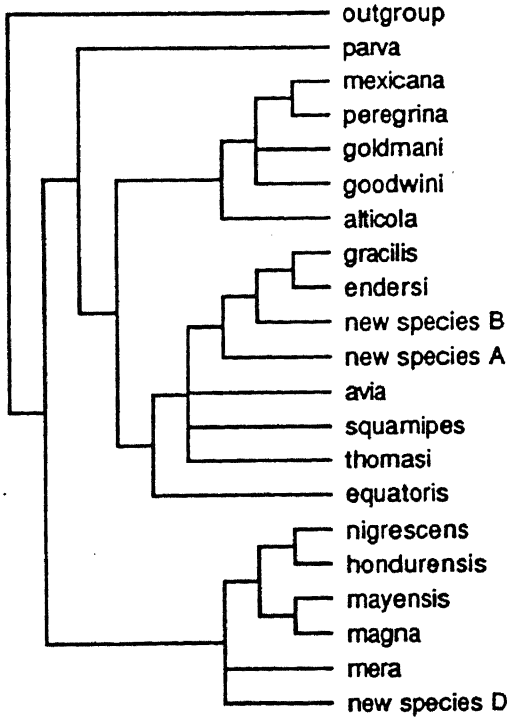
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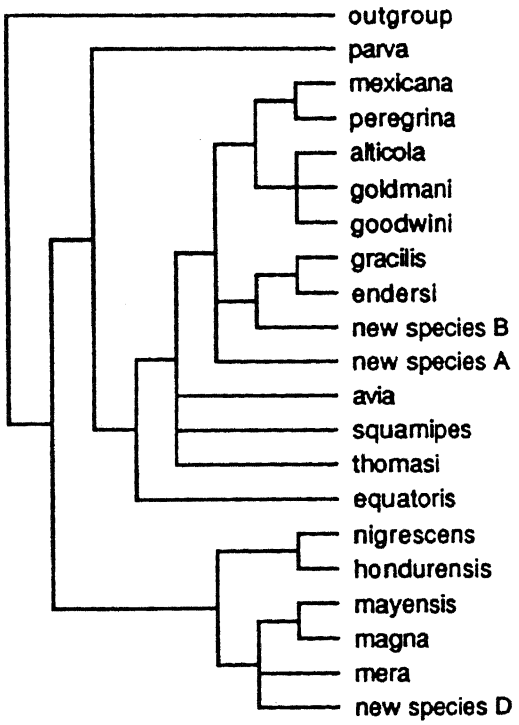
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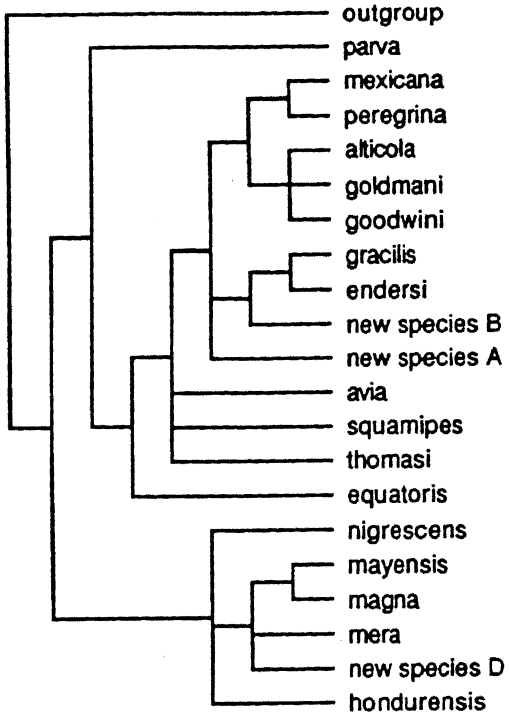
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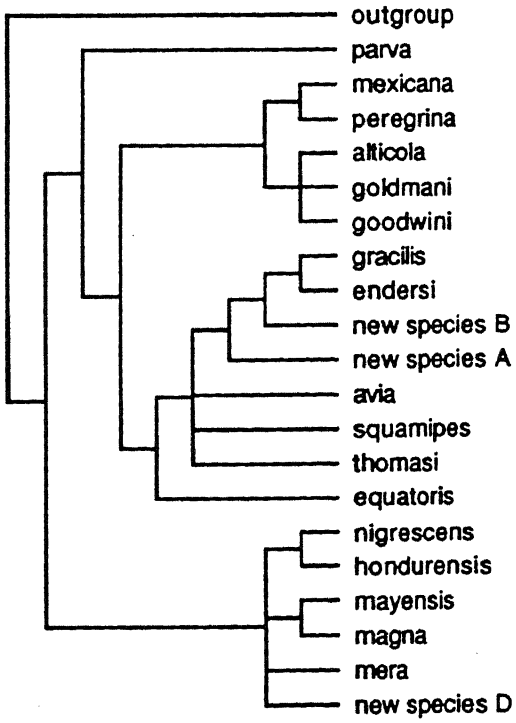
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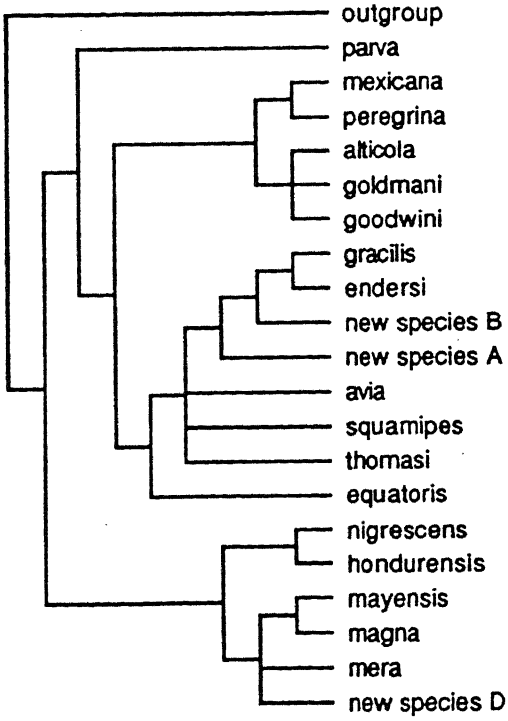
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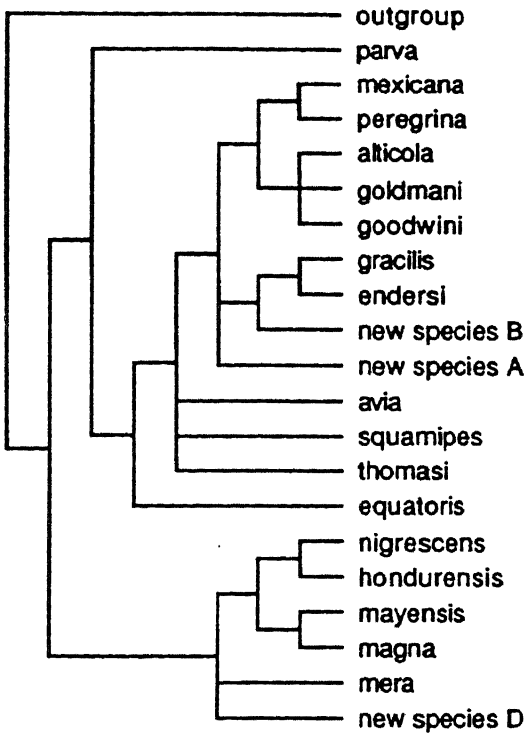
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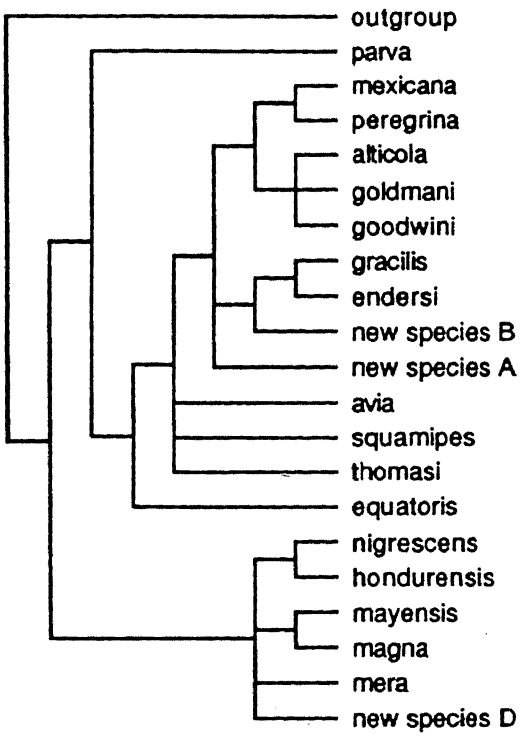
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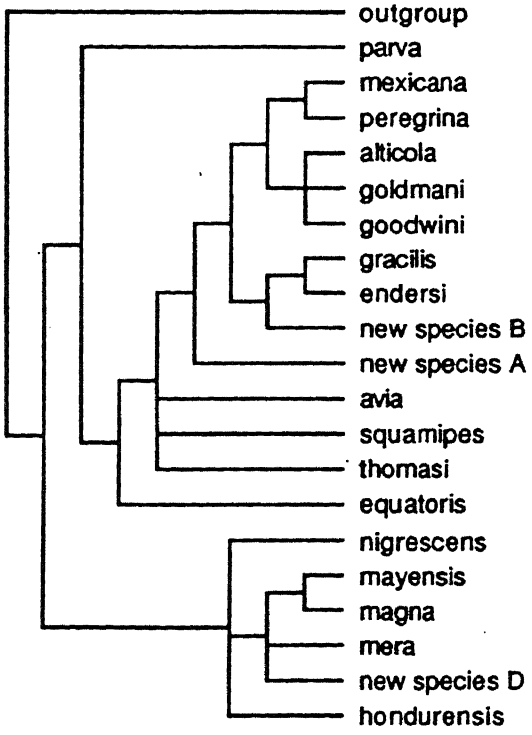
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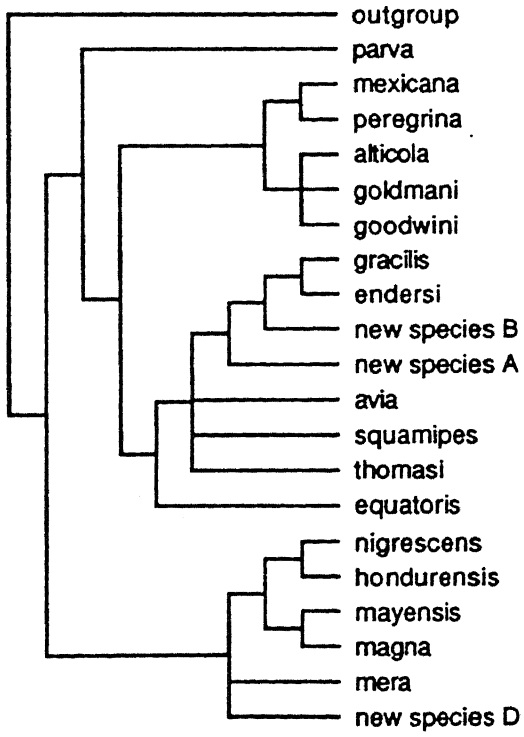
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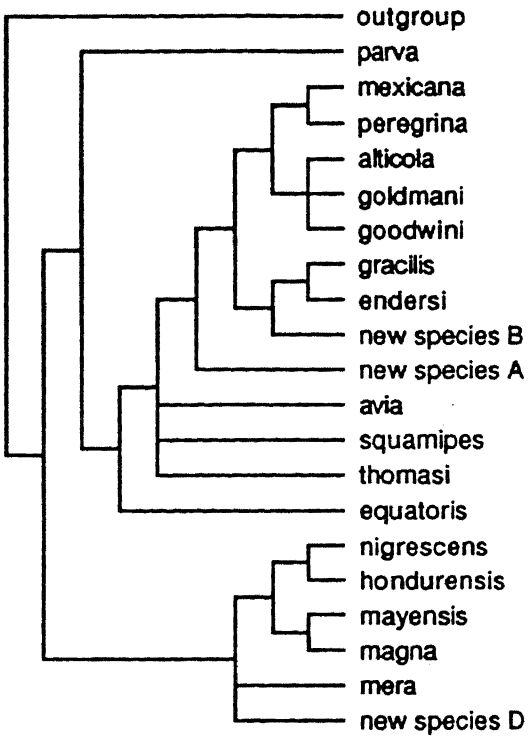
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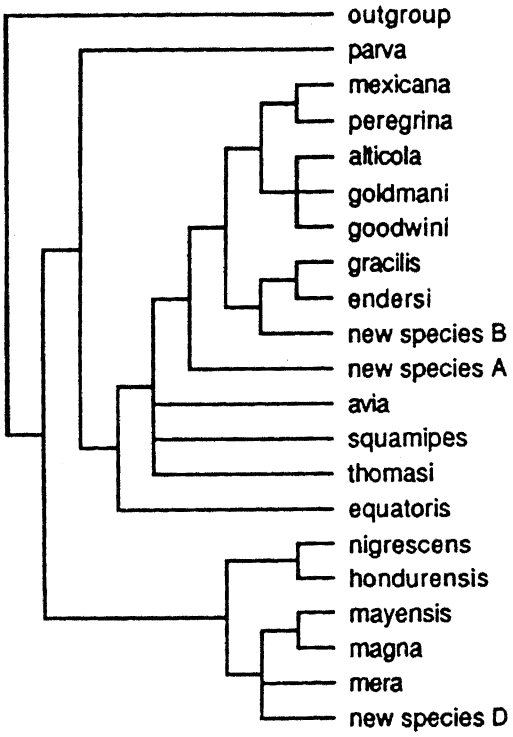
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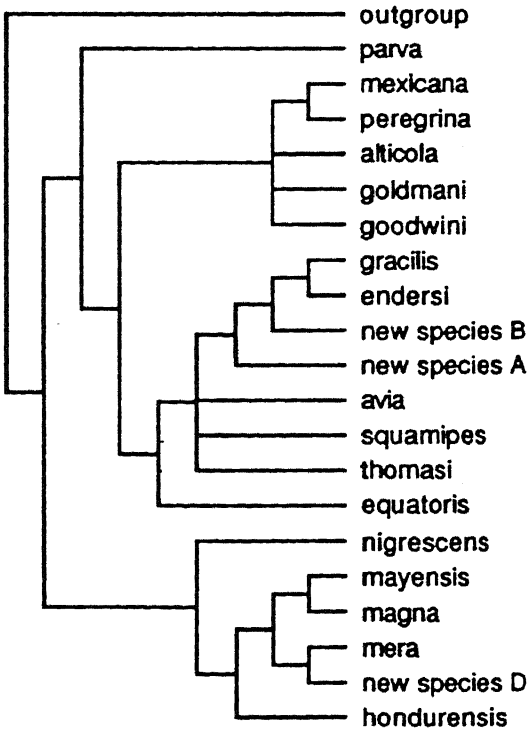
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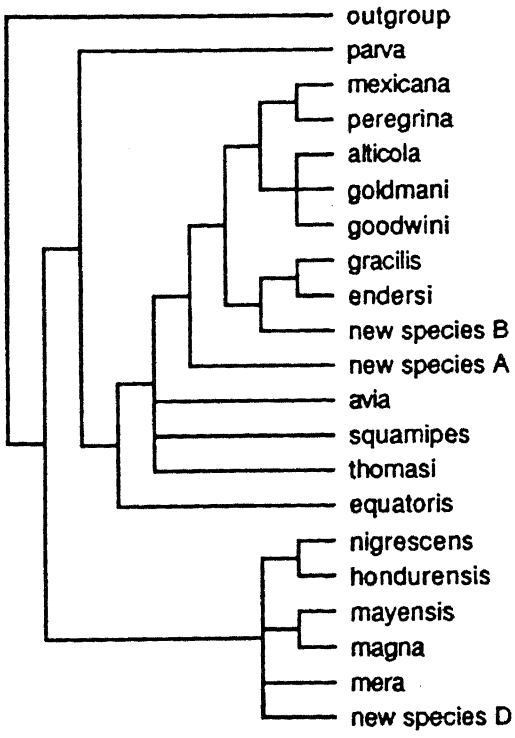
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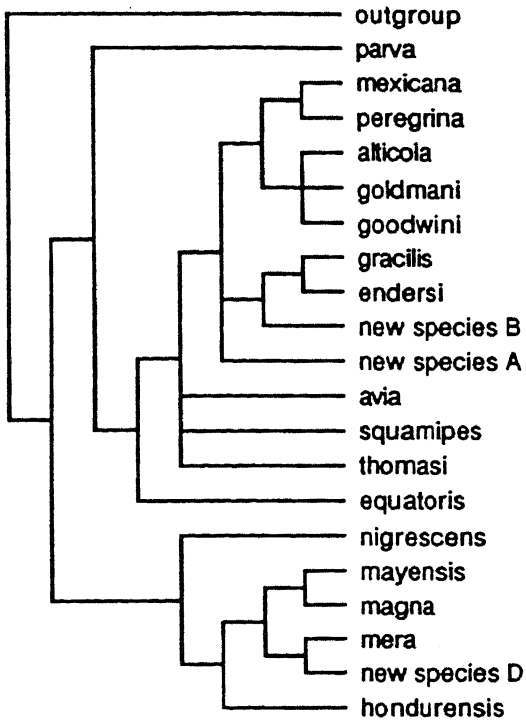
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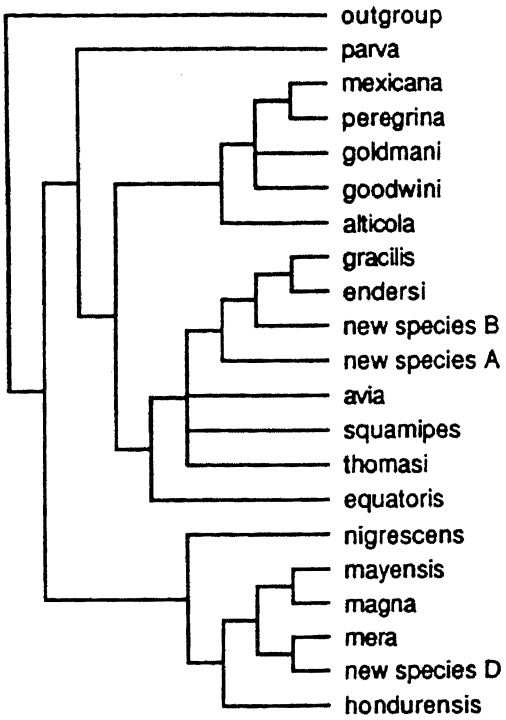
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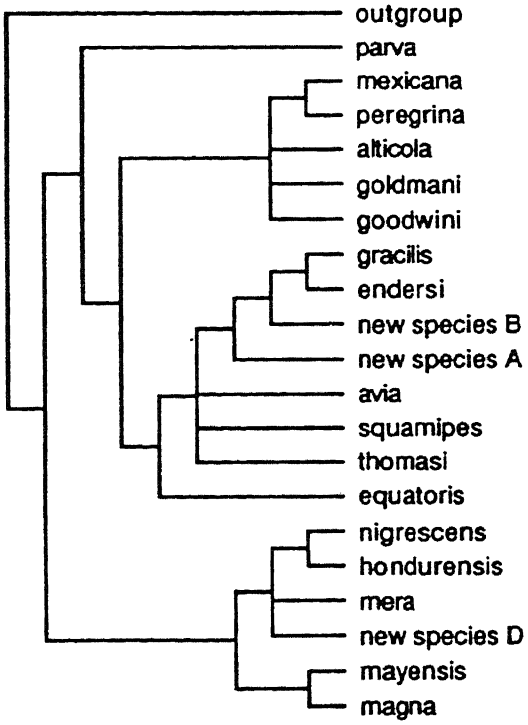
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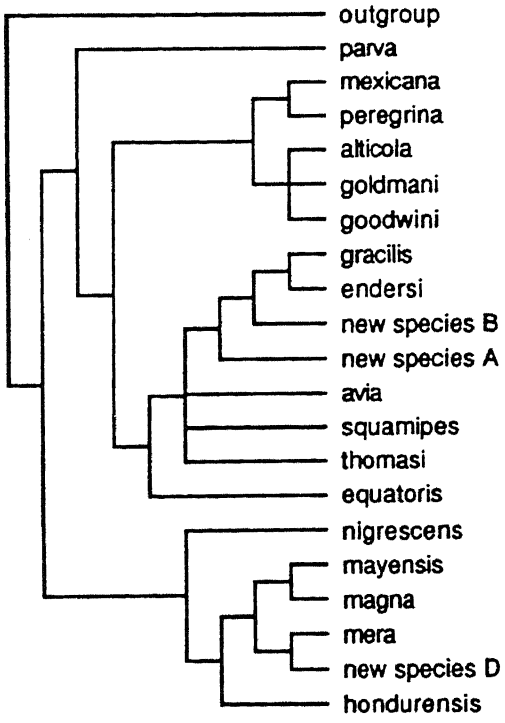
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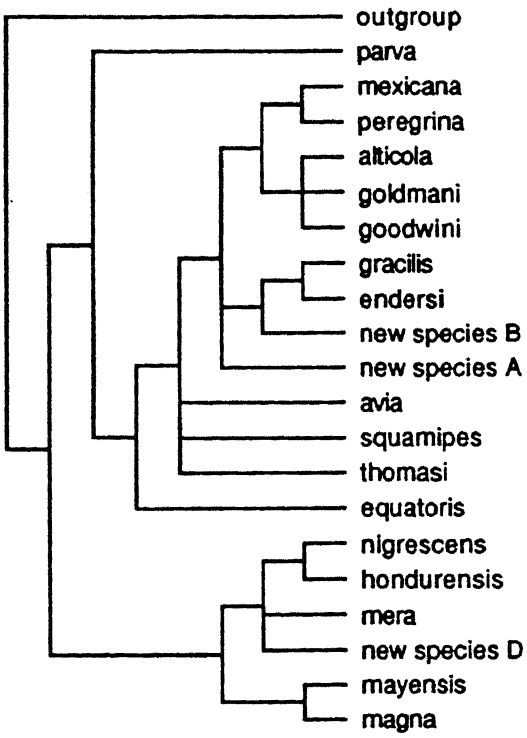
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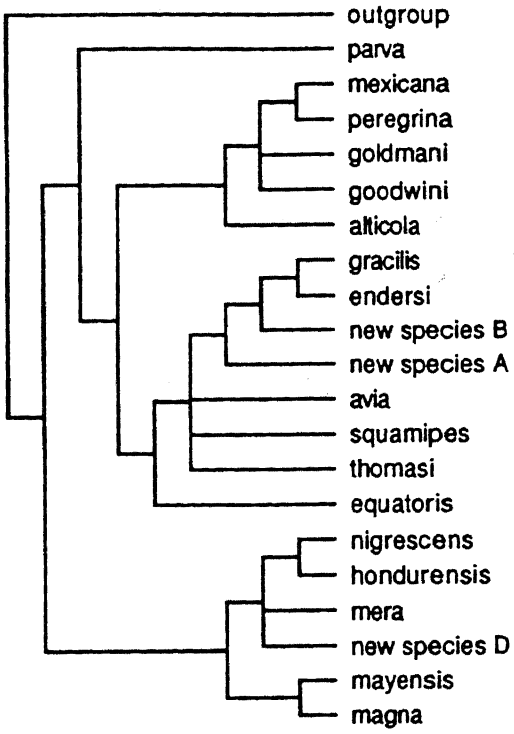
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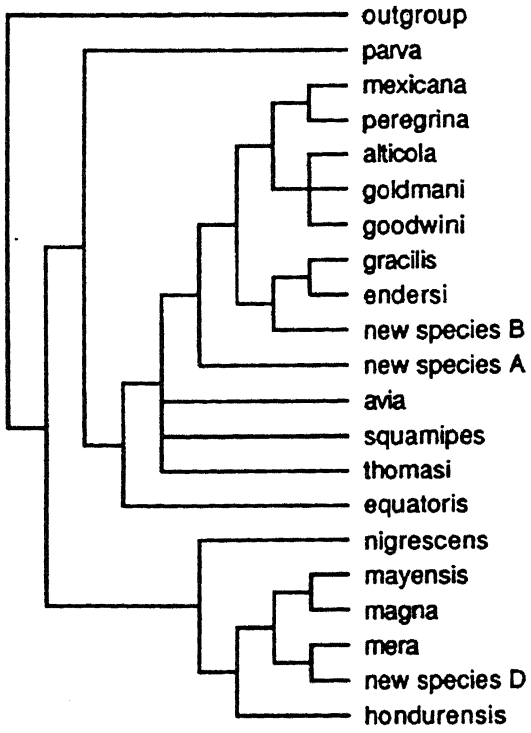
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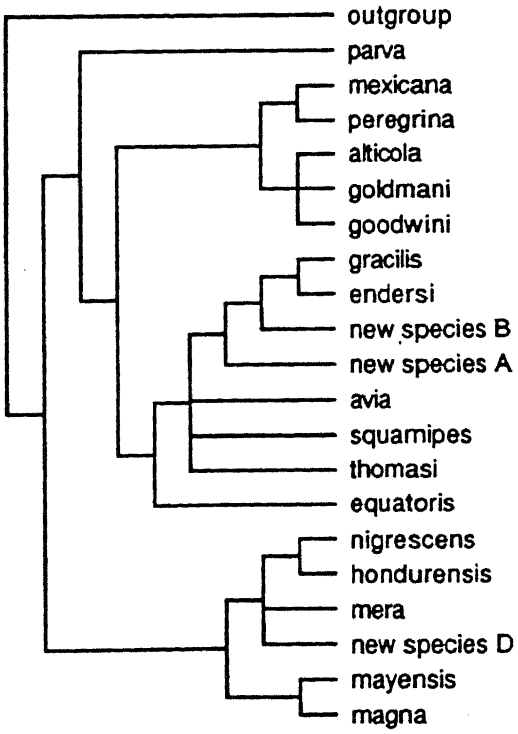
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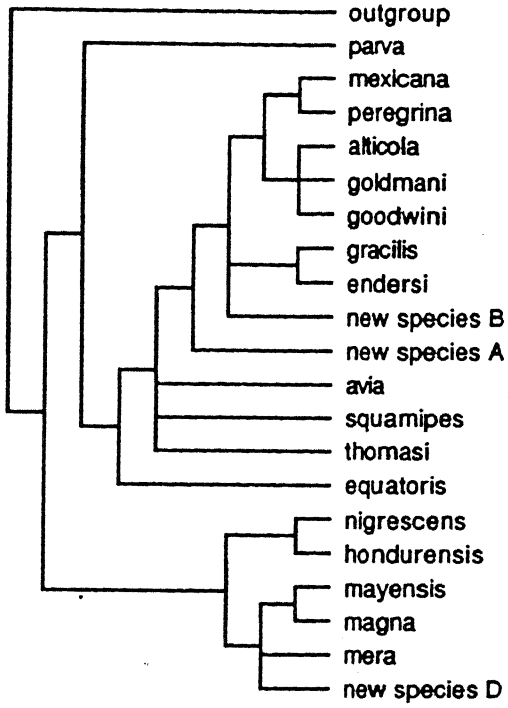
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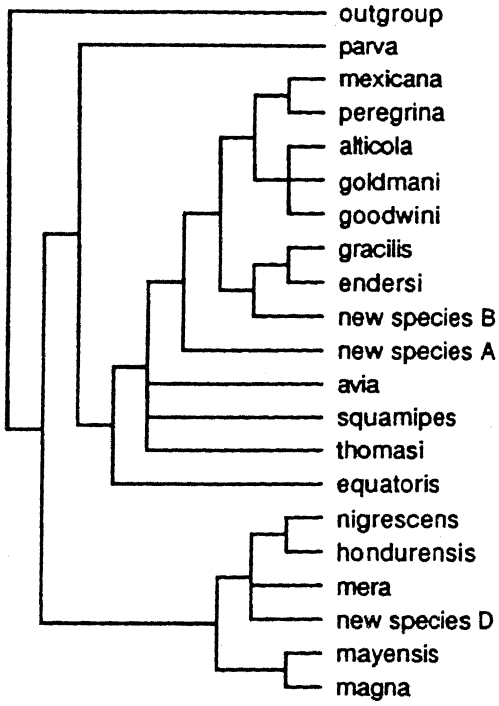
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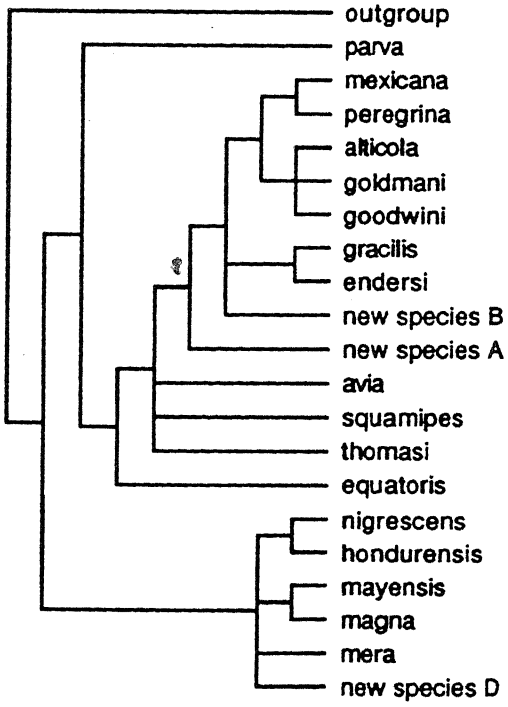
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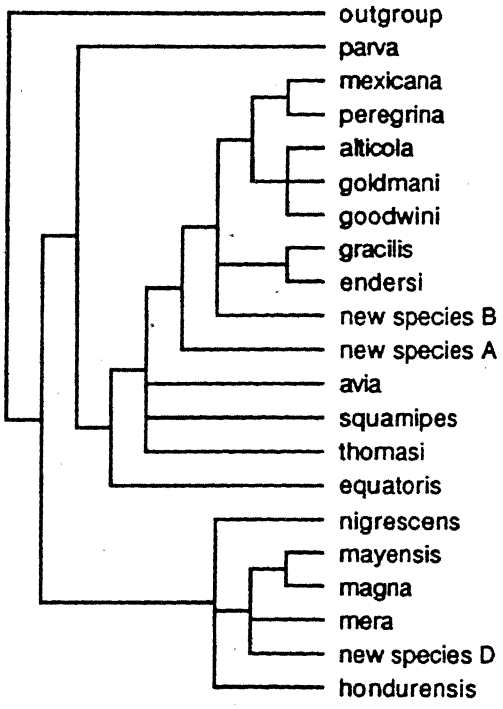
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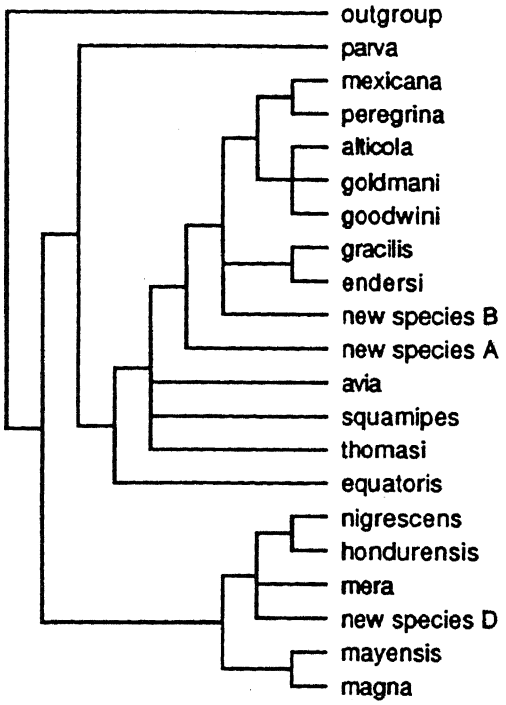
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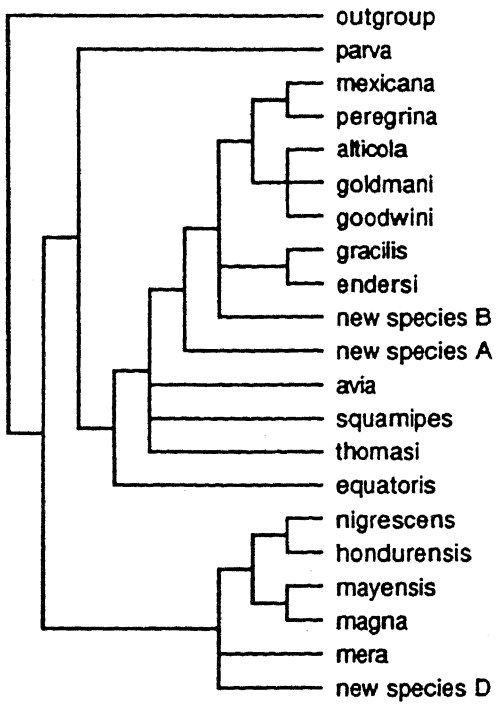
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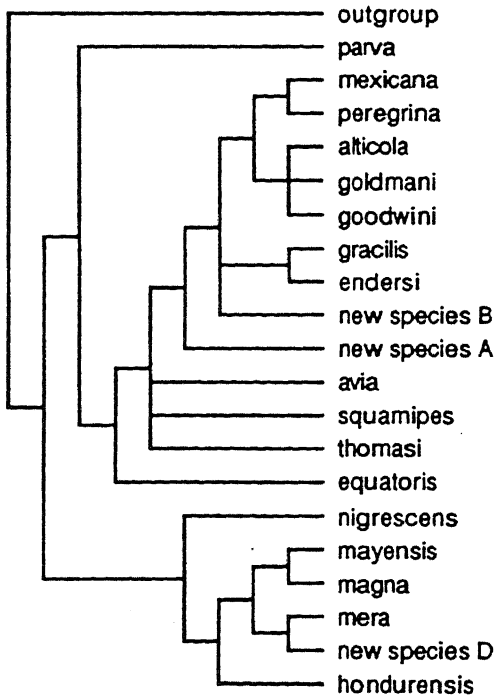
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